This thesis is accompanied by a box of microscopic specimens and a case containing 44 illustrative plates (142 figures)
J.M.M.

On the Comparative Anatomy

of

The EIGHTH NERVE.

THESIS for the degree of Doctor of Medicine.

by

Jessie M. MacGregor, L.R.C.P. & S.E. M.B. & C.M.

Question of eligibility not yet settled. Referred to Professor Taylor. J.S.

Not eligible

And in competition for the Gunning Victoria Jubilee Prize in Zoology

~~if eligible~~

INTRODUCTION.

On the comparative Anatomy of the eighth Nerve.

The eighth or auditory nerve as it appears in the human being differs so greatly in its mode of termination and its connections from any other cranial or spinal nerve, and its study presents so many problems, that it seems desirable to attempt to obtain an explanation of its nature by the systematic examination of its development and relations throughout the vertebrate series. By the careful comparison of lower forms with higher, it will, it is hoped, be possible to throw some light on the difficult questions of the origin, relation and functions of the nerve as it appears in man.

In order to thoroughly understand the nerve it is absolutely necessary that the organ it supplies should be thoroughly comprehended, since, in this as in other cases, the nature of the organ, its development and modifications are the factors which determine the history of the nerve, and of the central nervous origin of the nerve also.

To attain this complete knowledge of the inner ear, its nerve, and its central nervous connections it is necessary to go back to the very earliest stages of their history and to trace step by step the gradual processes of development through which they pass in the vertebrate series.

The Auditory Organ.

There is now no doubt that the auditory organ (or inner ear) is closely related to the series of sense organs which is present over the surface of the head and trunk in fishes and certain amphibians, and is known as the series of "lateral line organs" or "canal-sense organs". The researches of Beard and Ayers have placed this beyond question, and long before their time the relation had been suggested by Leydig, Allis and others. ?! ?

These lateral line organs are essentially similar in structure to the ~~phyllogenetically~~ phylogenetically older end-buds, which are present in every vertebrate as little dome-like elevations, composed of several central cells with sensory hairs and a few peripheral supporting cells. These end-buds are scattered irregularly over the whole surface of the body in most fishes, are limited to the oral and nasal cavities in the dipnoi and amphibia; and in mammals are represented only by the taste-buds of the tongue, pharynx and palate. They are innervated by the dorsal sensory roots of the spinal nerves and of certain cranial nerves.

In addition to these "end-buds", the more highly specialised lateral line organs are present in fishes and aquatic amphibia. In their simplest form they are essentially similar in structure to the end-buds, as will be seen from the accompanying diagram, but they differ from the related organs in several particulars:-

(a) They are arranged in definite areas of the head and trunk.

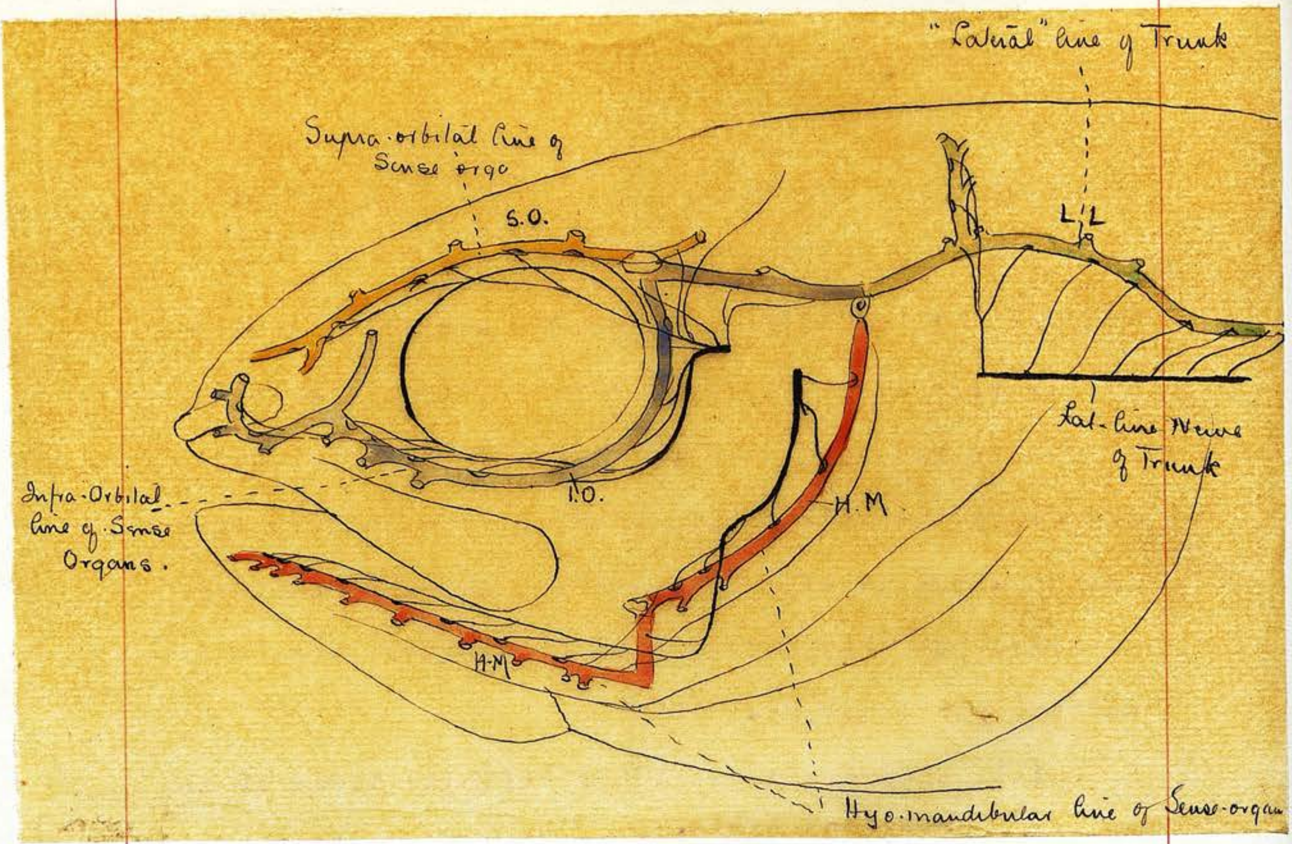
(b) They may become depressed below the surface, and covered, in "canals", when they are known as "canal-sense-organs".

(c) They acquire a special function, which, whatever its precise nature is undoubtedly concerned in equilibration.

(d) They are innervated by a special system of sensory nerves , which we shall call the eighth nerve system.

Lateral Line Organs.

In the most primitive fish, the amphioxus, these lateral line organs are represented by certain rod-shaped cells each provided with a hair-like process, which are scattered irregularly over the anterior extremity of the animal. It is in the true fishes, however, and the amphibian that the lateral line organs are present in their characteristic



Arrangement of the lateral line Organs.
(Ewart).

arrangement. In these classes they appear to follow a definite plan. On the head they form three main lines supra-orbital, infra-orbital and hyo-mandibular and on the trunk they are placed along one or more lines extending over the sides of the body throughout its whole length. In some fishes they are placed more irregularly on the trunk.

Although originally elevated above the surface of the epidermis they may, in certain fishes, become deeply placed and covered in by an arch of epidermis, of scales, or even of cartilage. In this latter condition, invariable for some fishes, they are known as canal sense organs. It is interesting to note that they remain superficial in the dipnoi, aquatic amphibia and all amphibian larvae, that is- precisely in those classes in which the life is not permanently aquatic, and further when the amphibian assumes terristrial habits these lateral line organs disappear. In permanently terrestrial forms they do not return, but those amphibians which become aquatic during the breeding season evidently acquire a new series of lateral line organs, which must either be developed de novo or be a recrudescence of the old ones.

When the lateral line organs become functionless and vanish the nerves supplying them also disappear, and thus a re-arrangement of parts is necessary in the nerve centres from which they arose. These changes will afterwards be seen to be of great importance as regards the eighth nerve, and will be fully described later. As regards the _function_ of these organs, all that can be said here is that they are evidently required for the aquatic life of the animal, since they are best developed in the purely aquatic fishes, irregular in the mud-fishes, and disappear in the amphibia when these become terrestrial in their habits. Experimental evidence as to their function has not hitherto been obtained, but it may be safely assumed that they are intimately concerned in the maintenance of equilibrium, probably by the perception of the density and the movements of the surrounding fluid.

The origin of the lateral line and auditory organs. The original source of the system of lateral line sense organs is not yet perfectly clear. Beard is of the opinion that they are developed from certain of the branchial sense-organs which were

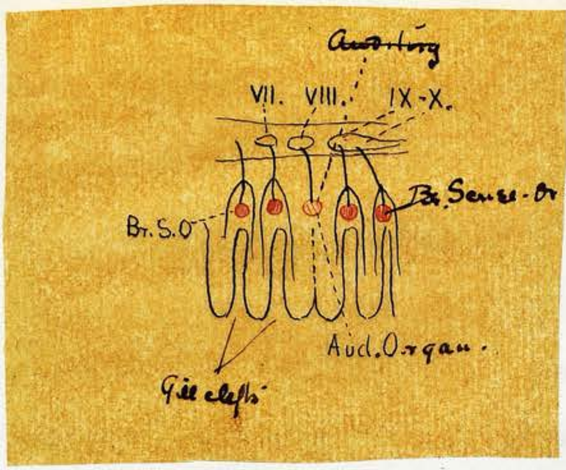


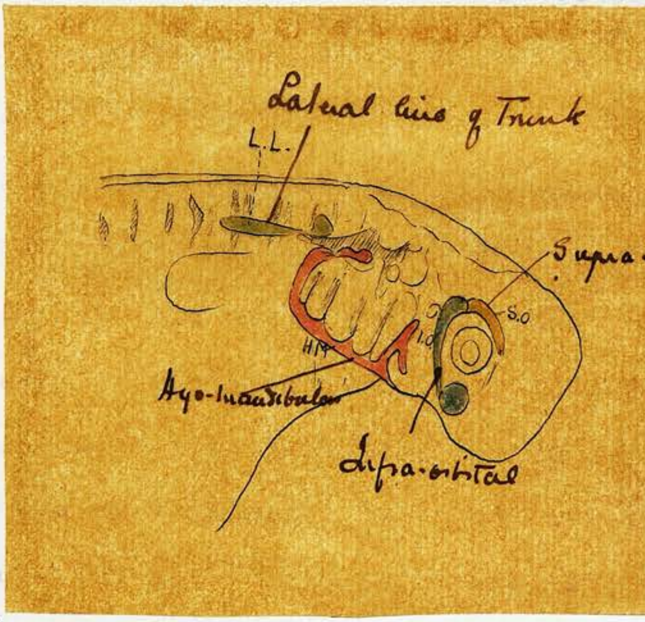
Diagram showing Beard's view of the Origin of the auditory and nerve.

originally present over each gill cleft of the embryo. He regards the auditory and olfactory organs as the only representatives, in the higher vertebrates, of these branchial sense organs, but considers that the whole system of the lateral line organs in fishes and amphibia is derived from the branchial sense organs which were originally present over the clefts supplied by the facial, glossopharyngeal and vagus nerves, a view with which Ayers and Professor Ewart agree in the main. Miss Julia Platt in a recent paper however, traces the origin of the auditory organ back to a still earlier stage. She shews that in the very early embryo of Necturus, the epithelial ridge which formed the neural crest is replaced by three parallel ecto-dermal ridges, dorsal, median and ventral, which run the whole length of the trunk, and two of which, the dorsal and the median, are continued with slight modifications, on to the head. These ridges, visible macroscopically, as faint lines give origin by proliferation of their deeper cells, to certain closely related sensory and nervous structures. From the cephalic portion of the median ridge the vagus and glossopharyngeal ganglia are divided off, and the epi-branchial sense organs of this region are formed. From the cephalic portion of the dorsal ridge the supra-orbital chain of sense organs and part of the Gasseran ganglion are formed anteriorly, and the auditory sense organ is divided off posteriorly. The ridges seem to become exhausted, so to speak, in the formation of these structures and disappear, but at a later stage in the life of the embryo, the cells of the sensory structures in the neighbourhood of the auditory organ again begin to proliferate rapidly, and give rise to the lateral line system of the head and trunk. This system is formed by a growth forwards in to the head and backward over the trunk of a column or columns of cells which follow out precisely the lines of the original ectodermal ridges. The ear will thus be seen to be, as Ayers and Beard pointed out, an older structure than the lateral line sense organs,- a fact which explains its comparatively advanced state of development, while the lateral line system is still only in process of formation. It is not derived from the branchial sense organs, but appears at the same period, and while they are derived from the median epi-branchial ecto-dermal ridge, the auditory organ is derived from the dorsal ridge.

Before leaving this part of the subject a suggestion put forward by Assheton is worthy of mention. In describing the temporary ciliation in the very early embryoes of some amphibians he notes the fact that the cilia are strongest and best marked along certain lines, whose position corresponds to that of the future primitive ridges, and, therefore, also of the lateral line sense-organs in older embryoes. Assheton regards it as possible that these ciliated cells may be the fore-runners of the branchial sense-organs, and also connects the ciliated vertebrate embryo with the ciliated embryo so common among the invertebrates, looking upon the former as a link between the two great classes. If the connection between the temporary ciliated cells and the later sense-organs could be conclusively proved it would be interesting to find that the middle ear was an almost uninterrupted, though highly specialised development of the ciliated surface of the vertebrate embryo (in cases where ciliation is present) and might further, be a vestige of the still earlier invertebrate condition

Further development of the lateral line system.

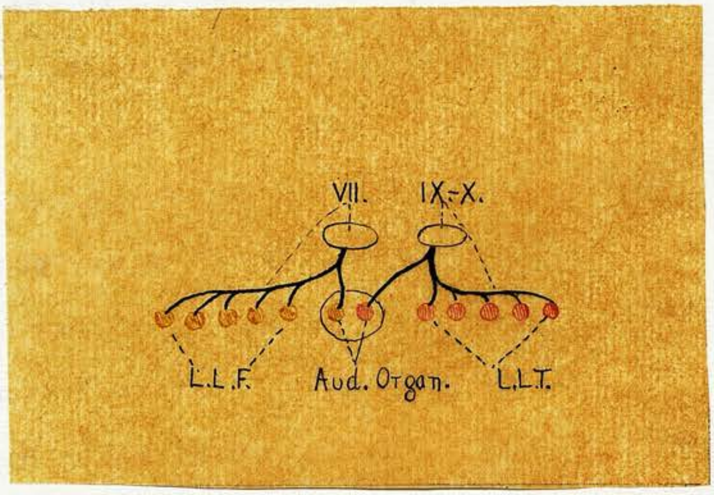
It was said above that the auditory sense organ was developed to a certain stage while as yet



Secondary ridges from which the sense organs are formed (Miss Platt).

there was no appearance of the great majority of the lateral line sense organs. There were however certain faint lines visible along the head and trunk in the position of the future sense organs, indicating the situation which these latter finally occupy. At a certain stage of development the sense organs already present in the areas anterior and posterior to the ear begin to proliferate rapidly and tend to grow forwards and backwards along these faint lines. In so doing, the growth is entirely due to rapid proliferation of sensory cells, which starts from these given points and invades the new territory as a solid column, which so to speak, ploughs up the ectoderm before it, but does not incorporate any of the structures through which it passes. The best description of the subsequent subdivision into separate sense organs and the development into the sensory canal organs is given by Allis and will be briefly recapitulated here, in so far as it enables us to understand the development of the auditory organ, which is itself simply a modified sense organ, similar to those of the lateral line. Before entering upon this description one fact must be noted, and that is that the column of cells which grows backwards and forwards from the auditory region in the manner just described does not avail itself of the sensory nerves of the areas it invades, but carries with it a nerve supply from the region from which it originated. The result is that the whole lateral line system, extending from snout to tail, derives its nerve supply from a centre in close proximity to, or identical with, the centre in the medulla for the auditory sense organ. Ayers regarded the nerves as derived from the facial and the glossopharyngeal and vagus nerves, but it is evident that the association with these nerves is merely extra-cerebral, the intra-medullary centres are distinct. This point will be fully discussed later.

Allis accepts the early derivation of the lateral line organs from the branchial sense-organs and figures the gradual extension of the solid band of cells along the various lines on which the sense-organs are to appear. At intervals on this band of cells small accumulations appear which eventually take shape as typical "sense-organs" with central hair cells and peripheral supporting cells. The intervening portions of the original band of cells become less marked, and the whole system is slightly depressed in a groove below the general surface. The sense-organ then begins to withdraw from the surface of this groove so that it becomes sunken in a recess, opening on to the general grove by a narrow mouth, and at the point where this mouth opens the lips of the grove grow up towards each other until they finally form an arch over the opening of the recess of the sense-organ. This arch transforms that portion of the grove into a small section of a canal with the sense organ placed near its centre. This process has been going on simultaneously, or nearly so, in all the adjacent parts, with the result that the lateral line now represents a series of short sections of canals. By a further growth these sections of canal tend to grow toward each other and fuse on their deeper surface, so that instead of having two free openings on the general surface, each sense organ has only two half-openings fused into one aperture, i.e. it is now placed on a continuous canal where there is only one opening or "pore" between every two sense organs. These external openings or "pores" do not remain single however, but by a growth inwards of their lips, each pore tends to become divided into two openings, and these again may subdivide, until the original canal may be connected with the surface by a large ramification of smaller canals opening as "pores" free on the surface. These



Ayers view of the origin of the
Auditory organ and nerve.
Showing original double sense-organ of ear and
supposed origin of auditory nerve from
the facial and vagus nerves

pores, canals and sense-organs constitute the system of "canal-sense organs". The general tendency apparently is for the sense organ to recede from the surface, with which it remains connected by the simple or complicated series of canals terminating as "pores" on the surface.

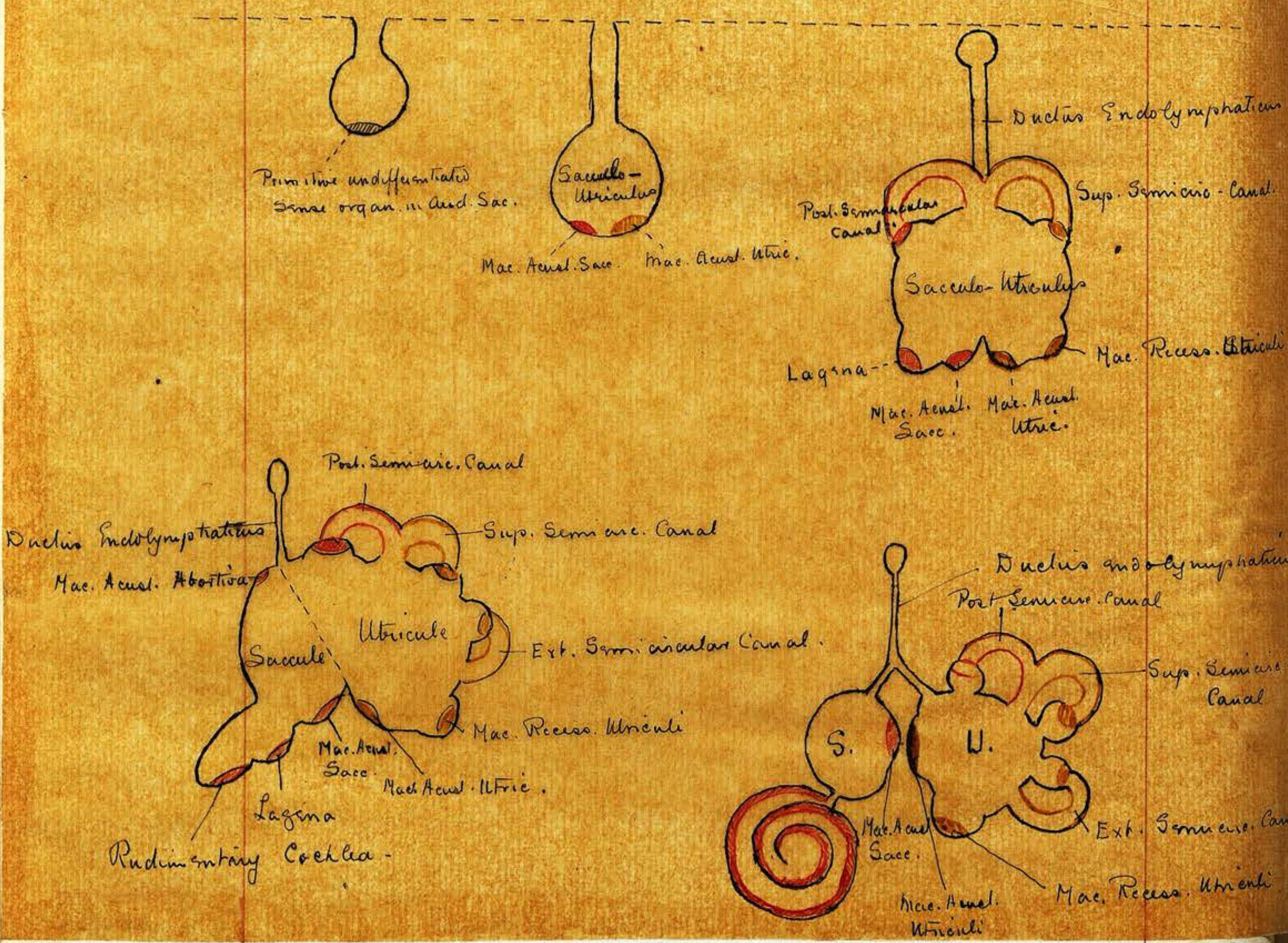
The development of the Auditory Organ.

Having studied the mode of formation of these canal sense organs it remains to be seen in how far the auditory organ resembles them in its mode of development.

In his masterly paper, Ayers suggests that the inner ear is formed from two of the lateral line sense organs which have become cut off from the remainder of the series. He is of the opinion that these two organs were originally situated between 16 and 17 of the remaining lateral line organs as figured by Allis, just at the junction of the head and trunk, and were placed partly in the area supplied by the facial nerve, and partly in that supplied by the glossopharyngeal. He bases this opinion on the double character of the organs of the inner ear, and partly on its supposed double nerve supply by the VII and IX nerves. As however

Miss Platt has shown that the auditory organ is an older structure than the lateral line sense organs; and as it is now generally allowed that the whole system of lateral line systems and the auditory organ derive their nerve supply from one common source, entirely independent of the facial and glossopharyngeal nerves proper, Ayers theory is no longer tenable. The auditory organ must therefore be regarded as a direct formation from the dorsal ectodermal ridge of the early embryo, and as an older and permanent representative of a system of sense organs of which the lateral line system is a later and temporary development. The primitive auditory organ rapidly recedes from the surface, and either divides or is originally double, since in its earliest known stages it consists of two sense organs, enclosed in a pit or recess, which opens by a pore on the groove of the lateral line - the sac thus formed continues to recede, until the canal uniting it with the surface becomes elongated. At the same time the epidermis on the surface tends to grow over the pore, until the latter is closed in and obliterated, the narrow canal, the future <u>ductus endo-lymphaticus</u>, ending blindly below the surface. The auditory sac thus becomes completely separated from the surface, and now constitutes an isolated

Showing Ayers view of the development of the Auditory organ.



organ. (These changes are illustrated in figure) In the lampreys and in some elasmobranchs the pore never becomes closed, so that the auditory organ is in free communication with the surface of the body throughout life, a primitive condition in which is maintained permanently the similarity between the auditory organ and the lateral line organs. In these fishes the pore of the auditory organ forms one of a series of similar pores belonging to the simplex lateral line sense organs. While this process of recession has been going on, the sense organs within the sac have begun to extend and to develop new sense organs in the same manner as did the lateral line chain on the surface of the body. The two sense organs in the sac may be regarded as Ayers suggests as rudimentary saccular, (macula acustica sacculae) and utricular organs (macula acustica utriculi) which finally appear in the higher stages as organs of the saccule and cochlea, and of the utricule and semicircular canals respectively. From each of these two rudimentary organs a band of cells grows out, and subsequently becomes divided up into various secondary organs as will be described immediately. The important point here is that the mode of growth is exactly similar in the organs within the auditory sac as it is in the lateral line system on the surface of the body.

At this point the auditory organ is merely a small sac isolated from the remainder of the lateral line and containing these two actively growing sense-organs, which give rise to "daughter organs" within the sac. From the saccular sense-organ,—the macula acustica sacculae,—there is given off the sense organ which afterwards becomes the crista acustica of the posterior ampulla and semicircular canal, and, later, the organ of the "lagena", the rudiment of the future cochlea is also given off. The crista acustica thus formed in its turn gives rise to a sense organ (the macula acustica abortive) which appears in the fishes, but atrophies higher in the scale until in most mammals it is completely abortive.

The macula acustica utriculi also gives rise to two "daughter" organs:- the crista-acustica of the superior semicircular canal, and the macula of the recessus utriculi. The crista acustica of the superior semicircular canal sub-divides in exactly the same way as the crista acustica of the posterior semicircular canal, but in this case the sub-division persists as the crista acustica of the horizontal (or external) semi-circular canal. It will thus be seen that the original sense-organs of the auditory sac have each extended in the same way as did the lateral line on the surface of the body, and the extension has subsequently broken up into separate sense-organs, ~~(Fig. ——)~~ most of which are functional in the human ear.

At one stage these organs are slight elevations on the inner surface of the sac, but, in accordance with the laws of their development they tend to become sunken below the general surface. Thus the lagenar organ and the organ of the recessus utriculi are depressed below the general surface in shallow pits, and the cristae acusticae become depressed within their respective ampullae.

Ayers has pointed out that the formation of the semi-circular canals takes place *after* the appearance of the ampullae, and has further suggested that their appearance is simply another proof of the conformity of the organs of the inner ear to the laws that govern the appearance of the canals of the related lateral line sense-organs. The semi-circular canals first appear as depressions or grooves (only two originally, since primarily there were only two cristae acusticae, the posterior and the superior) in the walls of the auditory sac, in connection with the ampulla, Subsequently these become bridged over by the growth of their lips to form an archway, in a manner similar to that in which the primary sections of canals on the surface of the body were formed. The superior semi-circular canal subsequently divides when the crista acustica of the external or horizontal canal is formed and its ampulla appears. The posterior canal does not divide as there is no proper secondary crista acustica formed in higher vertebrates in this case. The semi-circular canals are thus exactly similar to the primary canals of the surface of the body; they arise in connection with a sense-organ of the lateral line; they open at both ends on to the epidermal surface of the auditory sac, which was once entirely in free communication with the surface of the body, their openings thus corresponding to the primary 'pores' of the superficial system of canal sense organs. There are only five such pores for the semicircular canals, although there are three organs, since the canals of the external and superior canals never become quite distinct, but are joined at their ends by a common duct opening into the utriculus, a condition which is a repetition of the fusion of the primary canals on the surface.

From this description it is evident that the semicircular canals do not all arise from the utricular organ as is generally stated, but that the posterior crista acustica takes its origin from the macula acustica sacculae. The subsequent ingrowth of the walls of the auditory sac which divides it into a distinct saccule and utricle takes place in such a manner that the ampulla and aural opening of the posterior canal are cut off from their original source and included in the utricle thus bringing them into close relation with the utricular system. Additional proof of the statement that the posterior semi-circular canal is of saccular origin is found in the fact, as Retzius has shown, this canal is supplied by a branch of the cochlear (saccular) nerve and not by the vestibular nerve, which supplies the remaining two canals. In fishes, certain amphibia and birds, the auditory organ consists of the saccule & utricle, (connected indirectly by the forked end of the ductus endolymphaticus) the three semi-circular canals and the lagena, a simple depression in the floor of the saccule containing a simple sense organ. In the higher amphibia, the reptiles and the mammals the lagenar depression extends until it forms a spirally twisted tube, the cochlea. The lagenar sense organ persists in reptiles and in the monotremes, but is lost in the higher mammals. From it a series of sense organs has extended along the cochlear tube which form an elevation along its whole length, the papilla acustica basilaris. On this papilla there are at first two ridges, a large and a small. In the higher reptiles the large ridge is developed into the proper auditory organ of these animals (the "sauropsid" auditory organ). In mammals though this larger ridge appears in the embryo, and even persists after birth in some, it is the smaller ridge which eventually grows into the specialised series of sense organs which form the organ of Corti, the functional mammalian auditory organ. The intermediate sauropsid organ and the primary lagenar sense-organ have both disappeared.

In this schematic description of the auditory organ no attention has been paid to the actual order of development, or changes in structure or position. The question has been approached purely with regard to the original source of the parts of the ear, as that is the only aspect of it which bears on the present work. In the normal development of the human auditory organ there are of course many short cuts and abbreviations of the process as represented here.

The ductus endo-lymphaticus.

Before leaving this part of the subject the history of the ductus endo-lymphaticus may be traced. This structure, as already mentioned was originally the tube connecting the auditory sac with the surface.

In higher forms it becomes cut off from the surface and ends blindly, a small sac, the saccus endo-lymphaticus. In certain teleosts and most amphibians the sac is very large and filled with calcareous matter. In anura it extends along the whole length of the vertebral canal giving rise to out-growths which extend through the intervertebral foramina and come into relation with the spinal ganglia. In reptiles the saccular end of the duct is placed close under the roof of the skull beneath the parieto-occipital suture. In ascalabota it emerges from the cranial capsule and forms a large much folded sac sending finger like processes to the anterior surface of the vertebral column, the pharynx and even the orbit. In birds it does not leave the cranial cavity, and in mammals it passes through the petrous bone by way of the aqueductus vestibuli to end blindly beneath the dura mater of the brain.

Widersheim mentions that in certain fishes the auditory organ is brought into relation with the air-bladder by means of a chain of small ossicles, something akin to the ossicles of the middle ear in the mammal (the Weberian ossicles) and that in other fishes there are connections similar but less elaborate. This mechanism evidently serves to communicate the state of the tension within the air-bladder to the auditory organ, and its presence lends support to the view that the greater part of the apparatus of the inner ear in these forms continues to fulfil its primary mechanical functions of estimating changes of pressure in surrounding parts.

The origin and development of the Eighth nerve.

Having thus traced the history of the auditory organ from its most primitive stages it remains now to follow out the history of the auditory nerve in a similar manner. It will be remembered that in the very early embryo the edges of the neural plate are thickened so as to form an elevation, the neural ridge on each side of the plate. This thickening takes no part in the formation of the spinal canal proper, but as the lips of the plate approach and finally fuse, the neural ridges are combined to form a single ridge, which becomes cut off from the spinal canal and afterwards takes a great part in the formation of the posterior ganglia. This ridge is replaced in slightly older embryoes by the three long ridges of the ectoderm already described which are represented in the head region as dorso-lateral and epi-branchial. These ridges give rise to the entire sensory apparatus of the head by a process of transmigration of their cells into definite areas. The superficial cells may be altered directly into sense organs, and the deeper cells of the ridges form the ganglia of the dorsal sensory cranial nerves. The process is similar to that which occurs in the formation of the ganglion of a dorsal spinal nerve root. The cells of the original neural crest grow downwards, on each side of the cord and fuse in two places according to v. Wihje, Miss Sheldon and Miss Platt, with the sensory ectoderm, from which cells are separated off en masse to enter into the formation of the cranial root ganglia. From the most dorsal thickening (the dorso-lateral line of the head), the auditory organ and ganglion, parts of the Gasserian ganglion, the supra-orbital line of sense-organs and the nervus ophthal. profundus, which originally supplied these sense organs, are formed. From the epi-branchial or median ridge, the ganglia of the IX, X, part of the Gasserian ganglion and the ganglion of the lateral line nerve to the trunk are formed, with, in addition, certain sense organs. At this early stage it is probable that the dorsal cranial nerves are "sensory" in their nature but have not as yet adapted themselves to any specialised sensory function, and are therefor as yet undivided into nerves of common sensation and of special sensation. The further development of the embryo, however, brings with it the development of special organs, and therefore entails a specialisation of the corresponding nerves. The sensory organs with which we are concerned at present are the auditory and lateral line organs,—the latter series is of interest here in so far that, when present, its nerve bears an intimate relation to the auditory nerve proper, the whole system being known as the acustico-lateral system. The eighth nerve, in the vertebrata which possess a lateral line system, is therefore formed by the nerve to the auditory organ and a super-added nerve, or nerves, to the lateral line organs. These nerves end in a centre in the medulla which is generally known as the acusticum or tuberculum acusticum, a somewhat inappropriate name, which is likely to be confused with the tuberculum acusticum of the mammalian medulla. The nerves which emerge from this common centre are distributed exclusively to the auditory organ, and the lateral line sense organs (and also to certain allied organs). After emergence from the medulla the the lateral line nerves become associated with the facial, the glossopharyngeal and the vagus nerves, but this is merely an association. Unfortunately it has led however to much confusion since the lateral line branches were accepted as integral parts of these nerves and described as such. There is now absolutely no doubt that the facial and vagus nerves are quite apart from the acustico-lateral or eighth nerve system, serve perfectly different functions, terminate in independent centres in the medulla, and form different intra-cerebral connections. In the vertebrata higher than the amphibia the lateral line portion of the eighth nerve disappears, and there is a gradual increase in the importance of the auditory portion which becomes more and more markedly divided into two roots, cochlear and vestibular, as the cochlea of the inner ear becomes more and more specialised. The intra-cerebral connection of the nerve also becomes more complicated as the cochlear system increases. The vestibular or semi-circular-canal nerve apparently maintains the same relations unaltered throughout the whole vertebrate series, a fact which is in harmony with the other fact, that above the cyclostomes the organs of the semicircular canals also remain the same throughout the whole vertebrate series. It is only the cochlear portion of the ear which develops further and entails a corresponding increase in complexity of its cerebral connections.

The conclusions to be derived from this general introduction may be briefly stated as follows:-

The auditory organ, ganglia and nerves are derived from the dorsal primitive ridge of the embryo, and are closely associated with the system of lateral sense organs and nerves which appear later, and is only present in the lower vertebrates. In higher forms the lateral line system entirely disappears, but the auditory organ system continues to increase in importance. This increase is due to the great specialisation of the cochlear and saccular portion of the auditory organ, which entails an increase in the medullary centres of the nerve, (the cochlear branch of the eighth) which supplies it. In no case is there any actual close connection between this auditory system and the facial and vago-glossopharyngeal medullary centres, which form another completely separate system. The fifth nerve seems to be much more closely related to the eighth nerve than either of the others mentioned, and is probably analogous in some respects. There is however not space here to discuss this relationship fully.

Explanation of the nomenclature employed.

There has been as yet so little work done in the microscopic comparative anatomy of the nervous system that there is an unfortunate absence of a consistent nomenclature throughout the vertebrate series. Individual investigators working at different classes have in some cases applied different terms to the same structures and in other cases have employed the same term for totally different structures. This is especially true of the medullae of the fishes, in which great confusion has risen with regard to two most important points, viz:- the centres and roots of the fifth and of the seventh nerves. With regard to the first, the term "lobus trigemini" has been applied to a certain structure present in the ganoids and in the teleosts, but in the former it is a centre for the lateral line nerve, and in the latter it is the sensory (vagal or fasciculus communis) centre for the seventh nerve, in neither case has it any connection with the fifth nerve. In the elasmobranchs a nucleus analogous to the "lobus trigemini" of ganoids is known as the "corpus restiforme", also a wrongly applied term. The structure in ganoids and teleosts will be called here the lobus linear-lateralis, and that in teleosts the vagal nucleus of the seventh nerve, or the fasciculus communis nucleus.

The second point is the conflicting accounts that have been given of the various roots of the seventh nerve in the fishes and amphibia. It must be recognised that the so-called seventh nerve of older writers was in reality a "nerve complex" consisting of a motor root and an associated lateral line root. A third root, the vagal or fasciculus communis root, was usually ascribed to the fifth nerve (Mayser, Goronowitsch) The conditions are much simplified if the seventh is regarded as consisting purely of a motor and a vagal or fasciculus communis root, and the lateral line contingent which it receives subsequent to its emergence from the medulla be referred to its proper relation with the nucleus. The sketch given above will explain the arrangement of the parts, which is now accepted as correct.

In the following pages I have purposely refrained from using the names applied to the roots of the fifth and seventh nerves by Goronowitsch, Mayser and Strong. The nomenclature of the first two was incorrect in some respects, and that of Strong is no longer necessary. In order to ensure that the precise meaning of the names employed may be made clear a brief account of the nuclei and connections of the eighth nerve in the human medulla will be given here.

In the human medulla the auditory nerve consists of two branches, the vestibular branch and the cochlear branch. These enter the medulla separately, and have separate nuclei, and different intra-cerebral connections. As is well-known the cochlear root, which develops later than the other, arises in the ganglion spirale of the cochlea and subserves the sense of hearing. The vestibular branch arises in the intumescentia ganglioformis Scarpae of the semi-circular canals and is generally regarded as part of the nervous mechanism for equilibration.

Within the medulla, the cochlear nerve divides into ascending and descending branches and ends in the anterior acustic nucleus and the tuberculum acusticum. From these nuclei secondary tracts pass by way of the corpus trapezoides (the "dorsal" path of Held), and probably by a portion of the striae medullares to enter the lateral fillet of the same and opposite sides either directly or after interruption in the nucleus of the corpus trapezoides, the superior olive or the accessory olive. The lateral fillet in its turn terminates in the posterior corpus quadrigeminum - thus possibly bringing the cochlear nerve into connection with the oculo-motor nuclei. The nuclei of the cochlear nerve are also connected with the tegmentum of the opposite side by means of arcuate fibres.

The vestibular root of the eighth nerve terminates in relation to Bechterews nucleus Deiters nucleus the inferior vestibular nucleus and in part also to the dorsal or internal nucleus of the eighth nerve. The fibres of the root divide into ascending and descending branches of which the latter are long and thick forming the conspicious bundles of the inferior root of the eighth nerve. They pass downwards internal and dorsal to the restiform body, the lowest bundles ending in close relation to the cuneate nucleus of the medulla. From the cells of Deiters' nucleus fibres pass inwards and ventrally. Some of these bend upwards in the posterior longitudinal fasciculus on both sides, terminating in relation to the oculo-motor nuclei, and a stronger contingent passes downwards, some joining the opposite posterior longitudinal fasciculus and entering the anterior column of the cord, other fibres passing downwards in the antero-lateral columns to the cord (vestibulo-spinal tracts. The nucleus of Deiters receives fibres which arise in the opposite roof nucleus of the cerebellum (the cerebello-vestibular tract). and this roof nucleus is in close relation with the cortex of the middle lobe by means of the sagittal fibres of the cerebellum. The tracts from the cord and posterior column nuclei end in the middle lobe, so that Deiters nucleus is thus connected with the afferent cerebellar tracts. Deiters' nucleus and probably also the dorsal nucleus of the eighth nerve are connected with the opposite median fillet by means of arcuate fibres crossing the raphe. (Bruce)

The cerebellum is connected with the cord indirectly by means of the fibres from the posterior column nuclei which enter the cerebellum by way of the corpus restiforme, and directly by the dorsal (or direct) and ventral cerebellar tracts. Another tract from the lateral columns of the cord, described by Ferrier and Turner as the lateral fillet tract originates in relation to the lateral fillet, from the posterior corpus quadrigeminum.

The cerebellum is also connected with the nuclei of the pons by the middle cerebellar peduncle and with the red nucleus and optic thalamus by the superior cerebellar peduncle.

This brief account of the eighth nerve in the human being is, as said above, merely intended to ensure that the names applied to the various parts may be clearly understood, and will be supplemented by a fuller description of the parts later. It will be understood that when the names applied to structures in the human brain are used for lower forms the structures so called are regarded as homologous, the use of ambiguous terms such as lobus trigemini, dorsal sensory facial root, tuberculum acusticum etc., will be avoided, and when the structures present in lower forms are unrepresented in the human being, the names commonly applied to them will be employed, unless, as in the case of the lobus trigemini, for instance, the name is obviously wrong.

Throughout the whole of this work the term "eighth nerve" will be used instead of auditory, or acustico-lateral nerve, and will be regarded as including the whole of the system which ends in the eighth nucleus, i.e., the auditory and lateral line nerves in fishes and amphibians, the cochlear and vestibular nerves in higher forms. When a special part of the eighth nerve is meant the special name cochlear, lateral line nerve, etc., will be used. In the same manner the whole nucleus will be referred to as the eighth nucleus, and its special parts knows as Deiters' dorsal, tuberculum acusticum etc., the last mentioned term being reserved for the portion of the nucleus known by this name in mammals. The term "eighth nerve" is probably in itself incorrect, but it has the double advantage of being already known, and of implying no physiological theory, as do such names as "auditory" or "acustic"- Kingsbury suggests "acustico-lateral system", but unfortunately such a term is only applicable to the lower vertebrates. The terms Acusticus-feld introduced by Ahlborn and 'acusticum' both of which have been applied somewhat indiscriminately will also be allowed to drop.

One other point is, that I shall make use of the terms dorsal and ventral, superior and inferior in describing the direction and position of structures. Superior and inferior are only correct when applied to the erect position, but they are preferable to caudal and cephalic, and it is easy to picture the animal with its cerebro-spinal axis in a vertical direction.

Results of Examination of various representative brains.

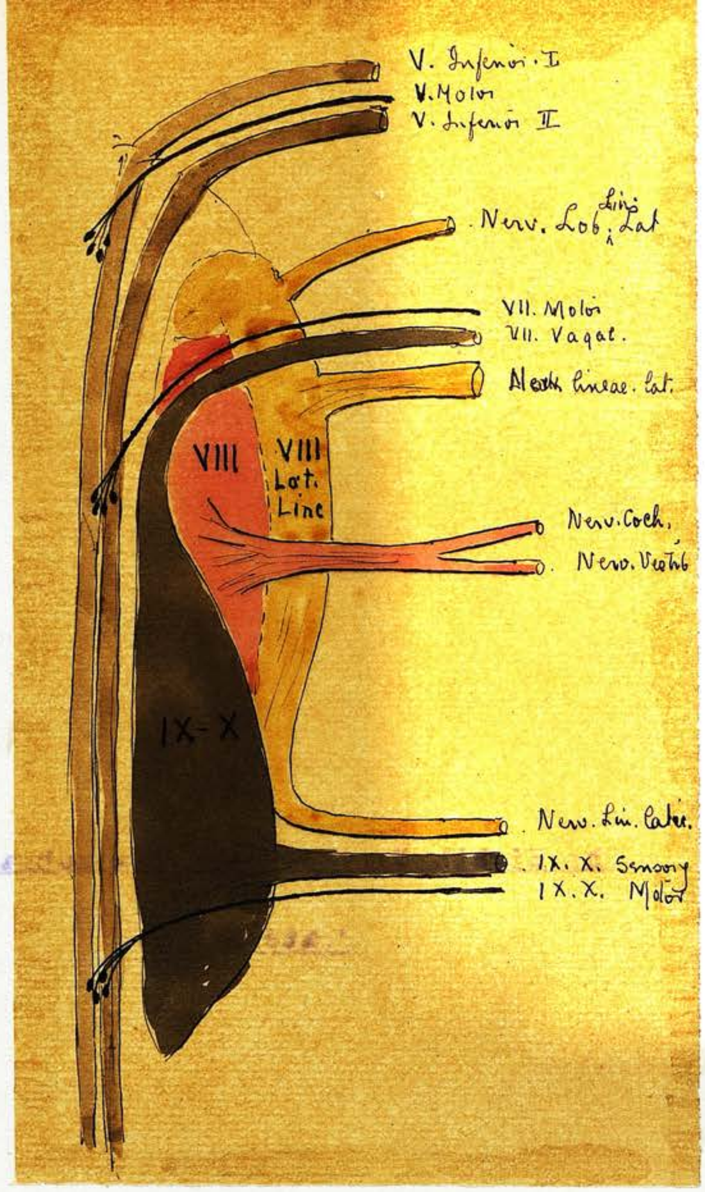
In order to compare the conditions present in the various classes of the vertebrata a series of representative brains were selected for examination. Those which have been illustrated here comprise an elasmobranch, and a teleostean among the fishes, an amphibian (the frog) a reptile (serpent) a bird (pigeon) and amongs mammals the opossum, calf rat, mole, cat and human foetus. Other forms were examined but not illustrated or described as the above were sufficient for my purpose. The majority of the specimens were hardened in Müllers fluid, and stained by the Weigert.- Pal method.

In all cases the investigations made by other workers on the same orders were studied, in order to avoid the error of drawing conclusions as to a class from the study of too limited a number of specimens.

The study of the selected types was made in the order of development, i.e., from the fishes to the higher mammals, so that the elasmobranch (the common skate) falls to be considered first.

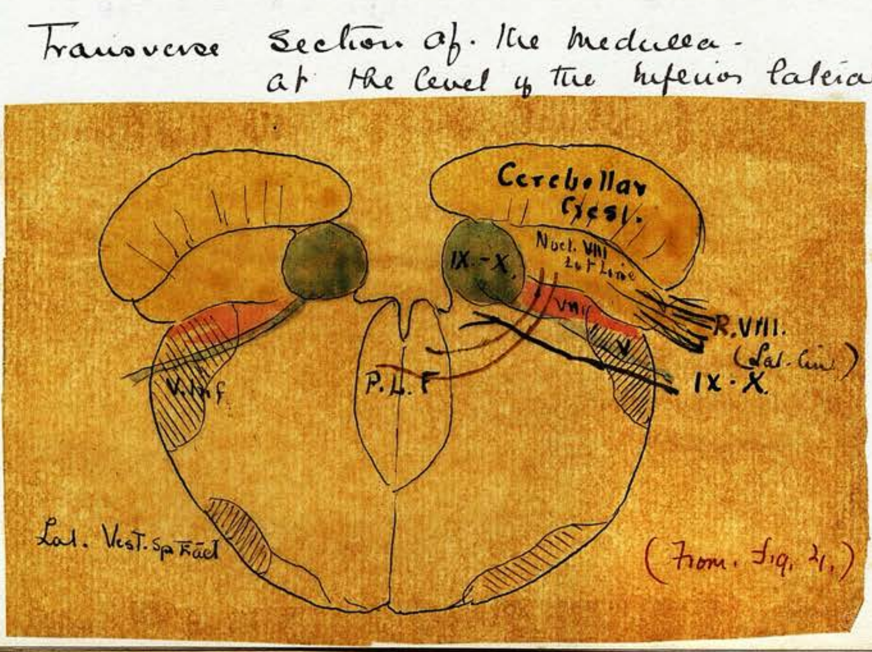
The Eighth Nerve in the Elasmobranch.

Plates. I - IX.



Scheme of VII. VIII. IX, X. Cranial nerves in the Skate.

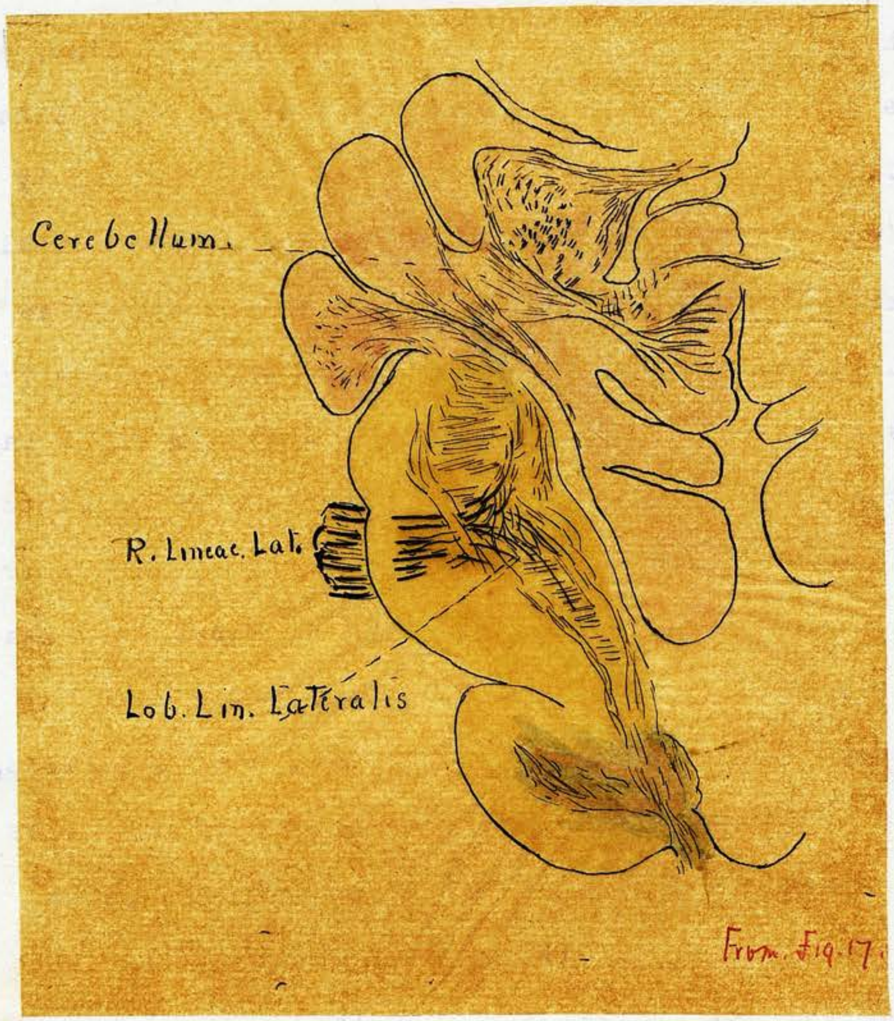
Transverse Section of the Medulla at the level of the inferior lateral line root.



The Skate.

In the skate the eighth nerve and its nuclei, including the lateral line nerves and nuclei, occupy a very large portion of the medulla. The system is placed in the lateral portion of the medulla, as the fourth ventricle is wide, owing to the fact that the cerebellum is broad and well developed, and tends to separate the more lateral parts of the medulla. The lowest appearance of the eighth nerve in the medulla is its inferior root, which forms a group of fibres, cut transversely in horizontal sections, lying dorsal to the inferior root of the fifth nerve (Fig. 3 - 4.). It lies here in close connection with the upper end of the posterior columns, the inferior root of the fifth nerve, and the nucleus and emerging roots of the vago-glosso-pharyngeal nerve. At a slightly higher level the group of fibres has increased in size, and is covered on its cerebellar aspect with a cap of cerebellar substance (the Cerebellar-leiste of Gorono-witsch). Recent investigators (Johnstone, Burckhard and others) have proved beyond doubt that this cap is identical in structure with the cortex of the cerebellum and contains the characteristic Purkinje's cells. I am in a position to confirm this as regards the skate. Above this point the nucleus of the eighth nerve continues to increase in size, and is seen to form an extension backwards, the dorsal portion being almost divided from the ventral by a dipping in of the cerebellar crest. This dorsal extension was originally described in ganoids as the lobus trigemini and the nerve which issues from it as a branch of the fifth nerve, - a view which has been since abandoned. The structure is undoubtedly in connection with the nucleus of the eighth nerve, and the nerve which arises from it supplies certain canal sense organs, therefore the nerve must be recognised as part of the nervus lineae lateralis, and the nucleus would be most correctly named, as suggested by Johnstone for Acipenser, the lobus lineae lateralis. (Figs 6.7.8. 9. 10. 11. 12.). The longitudinal frontal sections (Fig 17.) show the relationship of these two parts of the eighth nucleus very clearly. The root from the lobus lineae lateralis will be described later.

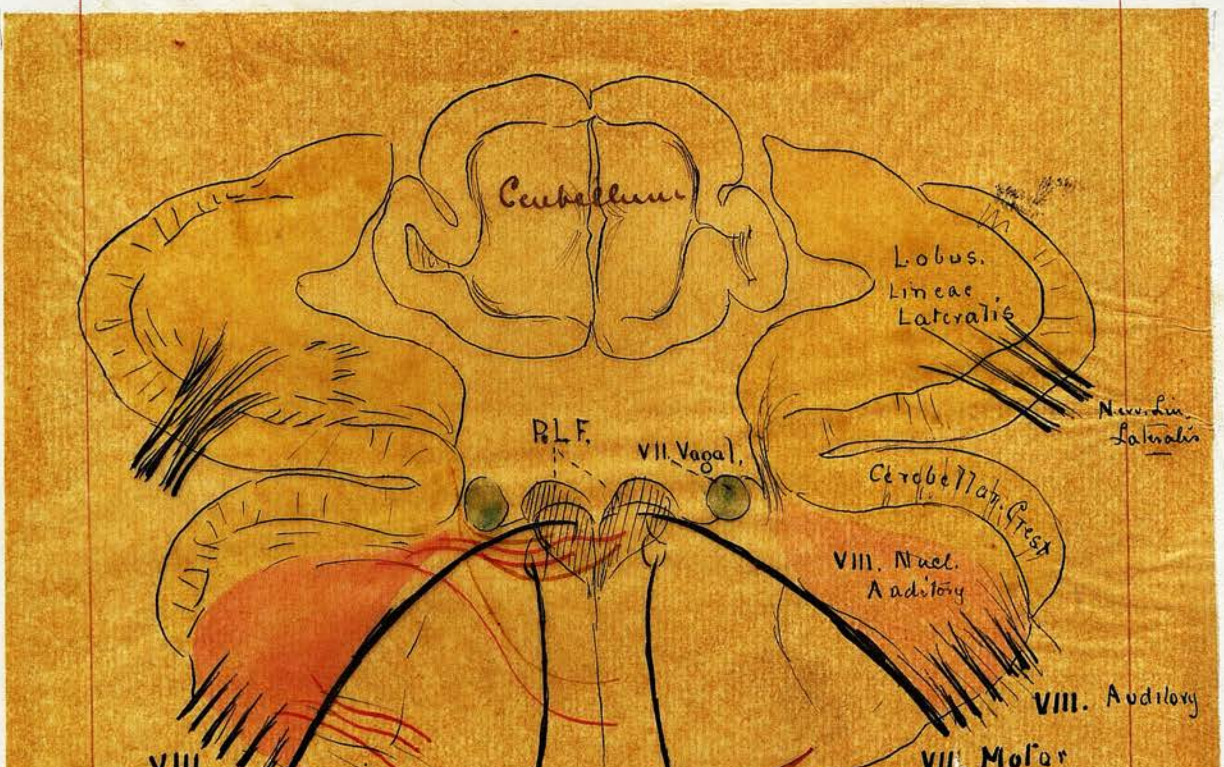
The lowest portion of the emerging root of the eighth nerve is seen escaping immediately ventral to the cerebellar crest in fig. 6 and again in the longitudinal section fig. 15.
This portion of the nerve becomes associated with the vagus, and supplies the lateral line sense organs of



Frontal Section - Showing lobus lineae lateralis and emerging superior lateral line root.

the trunk. This may be called the inferior lateral root line nerve.

The three succeeding sections (Figs. show the maximum development of the eighth nucleus which, with its cerebellar-crest, forms fully one third of the medulla proper, and if the lobus lineae lateralis be included, forms more than one half. The nucleus itself contains numerous bundles of fibres cut transversely or slightly obliquely, and separated from each other by fine horizontal fibres, which form a delicate network 'in and out' among the bundles. Nerve cells are plentifully present also, but are not shown by the Weigert-Pal process. It will be seen that the nucleus may be roughly divided into two parts, a dorsal part, immediately ventral to and connected with the cerebellar crest, and resembling the cerebellum in its structure, and a ventral portion. The area immediately ventral to the cerebellar crest receives the nervus lineae lateralis, while the more ventral portion is the end-nucleus of the nerve to the auditory organ. The emerging root of the eighth nerve at this level (fig. 8 & 9.) passes out in small bundles which pierce the dorsal portion of the inferior fifth. Separating the root bundles are other vertical fibres, consisting of the intra-medullary branches of the



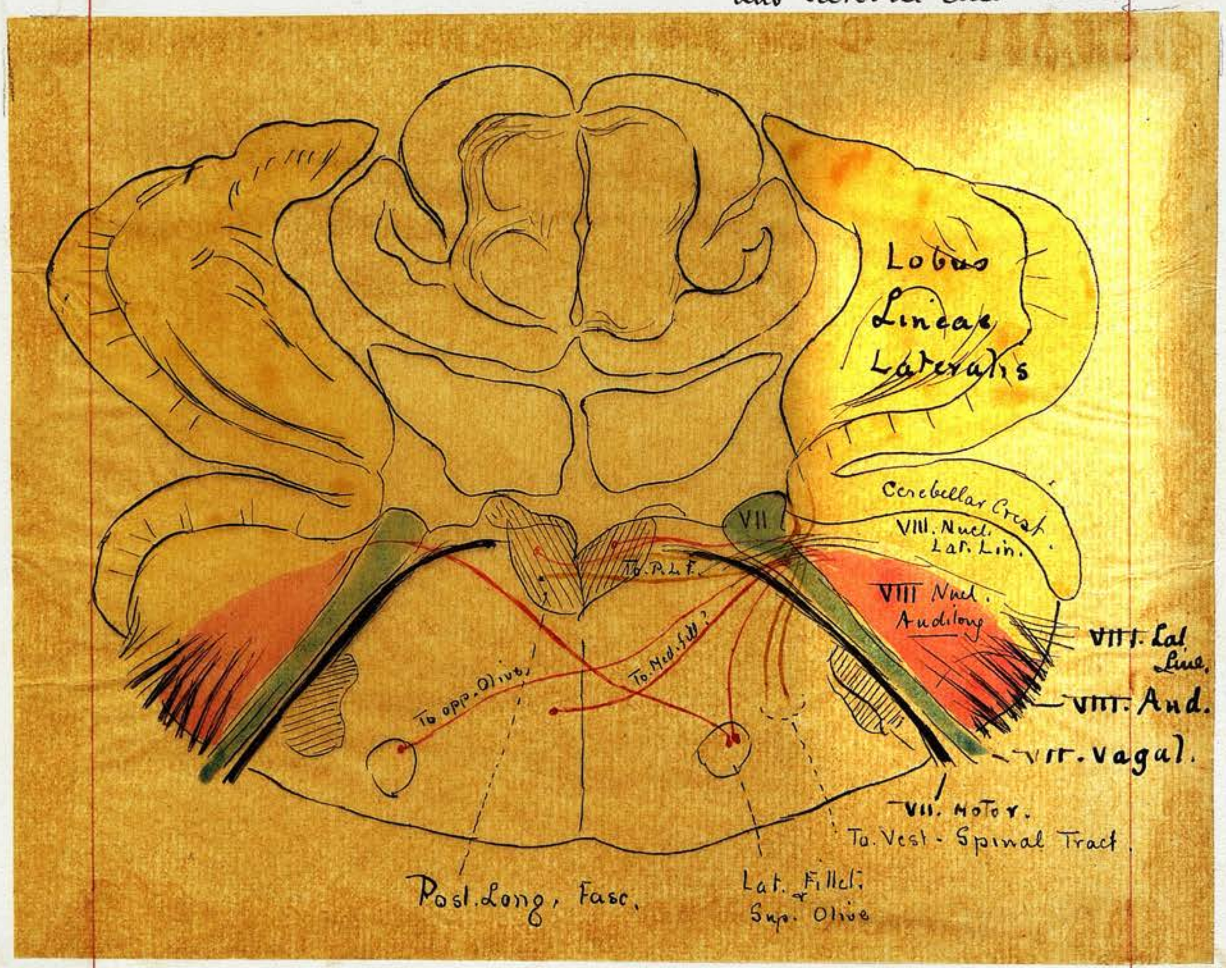
Transverse Section of medulla. Showing Lobus lineae Lateralis with Emerging nerve; auditory nerve proper etc inferior root of the eighth nerve itself. The root fibres divide within the medulla into ascending and descending branches (Fig. 16.13). The descending branches bend downwards, and constitute the inferior root of the eighth nerve, while the ascending branches pass upwards and terminate in relation to certain groups of cells at the base of the cerebellum, where this body joins the medulla, above the point of exit of the fifth nerve. These groups of cells are evidently in relation to fibres from both fifth and eighth nerves, and are probably analogous to the Uebergangs ganglion and Rindenknote which Mayser describes as present in bony fishes in this position.

The lobus lineae lateralis or dorsal portion of the eighth nucleus, has attained its maximum extent at this level. It resembles the more ventral portion of the eighth nucleus in structure, consisting as it does of an outer layer or crest, similar to the molecular layer of the cerebellum, with the characteristic Purkinje's cells. This layer thins off towards the more dorsal part of the nucleus, and ultimately disappears (fig. 12) Internal to the cerebellar crest, a large number of fibres may be seen passing in bundles in all directions. These bundles are derived from two sources, from the afferent nerve which enters the nucleus, and from the cells within the nucleus.

The nerve fibres enter the lobe in separate rootlets, piercing the cerebellar crest, and divide almost immediately into ascending and descending branches. The descending branches pass down a varying distance within the nucleus, the ascending branches pass upwards, to terminate near the base of the cerebellum. They do not seem to pass into the cerebellum directly. Many of the fibres of the root both ascending and descending terminate in relation to the cells present in the nucleus.

The cells of the nucleus are arranged in groups forming subsidiary nuclei and give origin to a great number of fibres, which after describing a curved course within the nucleus, unite to form a large bundle on its ventro-mesial aspect. This thick strand (figs. 8-12) passes out of the nucleus close to the lateral wall of the fourth ventricle, and, after spreading out slightly, skirts the inner margin of the ventral portion of the eighth nucleus proper and then divides into groups of arcuate fibres which spread out fan-wise within the formatio reticularis. The more dorsal of these fibres cross the raphe and enter the opposite posterior longitudinal fasciculus, while many others remain in the

Transverse Section - Showing - VII. nerve - (Motor and vagal portions)
" Probable paths of fibres from Auditory and lateral line nuclei



fasciculus of the same side. The fact that the fasciculus is much larger below this level than it is above indicates that the great majority of these fibres adopt a downward course within it.

The nerve from the lobus lineae lateralis goes exclusively to supply certain lateral line sense organs of the head. It was at one time regarded as a part of the fifth nerve, but its connection with the lateral line system is now generally acknowledged and is evident from fig.

The Seventh Nerve. On its ventral aspect the eighth nucleus proper is bounded for a short distance by the emerging motor root of the seventh nerve. This nerve rises in great part from cells in the immediate vicinity of the posterior longitudinal fasciculus and curves boldly through the lateral portion of the medulla, to emerge in close relation to the eighth nerve. (Fig 9. 10), this part of the nerve is purely motor. At a slightly higher level it is accompanied by a less deeply-stained nerve with which it is closely associated both in its intra and extra medullary course. This paler nerve arises from a small area of grey matter in the lateral angle of the ventricle which if traced downwards (figs 9- 5) is seen to be an upward continuation of the sensory nucleus of the vagus nerve, and may thus be regarded as analogous to the pars intermedia Wrisbergii of the human medulla. The name "dorsal root" of the seventh has been given to it, and Strong and Kingsbury describe it as the fasciculus communis branch, but so much confusion has arisen in regard to the so-called sensory roots of the facial nerve in fishes, that it is well to adopt a perfectly distinctive title. I have therefore called it the vagal root of the seventh nerve. This root is well seen in ganoids and teleosts as well as in elasmobranchs but becomes comparatively insignificant in higher vertebrates.

The branch of the lateral line nerve which arises close to and is associated with the seventh nerve has also been described as a dorsal branch and as a "supra-branchial branch", but it is better to retain the term, lateral line nerve and to recognise the fact that it is a part of the eighth which merely becomes associated with the seventh in its peripheral course: Strong fully recognised the complex nature of the so-called seventh nerve, but the names which he applies to its various roots, are difficult to remember, and it is unnecessary to recapitulate them here.

The facial <u>nerve</u> when fully formed, outside the medulla, would thus consist of motor fibres and two sets of sensory fibres, (viz:- a <u>vagal</u> and a <u>lateral line set</u>). Strong has shown that the lateral line branch is present in Tadpoles, but disappears in the adult frog and is not found higher in the vertebrate series. Therefore in all mammals higher than aquatic amphibia, the seventh nerve consists of purely motor fibres accompanied by some vagal fibres (the analogue of the pars intermedia). This part of the subject will be subsequently discussed in greater detail, as it is only necessary here to give such explanation of the nature of the seventh nerve as may serve to render its true relation to the other cranial nerves and nuclei clear.

Above the level of the seventh nerve the eighth nucleus becomes smaller and contains fewer groups of fibres. These pass upwards to end in relation to the fifth nucleus and to the cerebellum. It is bounded ventrally by the emerging motor root of the fifth nerve, in much the same manner as it was bounded by the seventh root at lower levels.

From what has been said it may be concluded that in the skate the nucleus of the eighth nerve is comparatively simple though large in extent. It contains the ascending and descending fibres of the entering roots of the lateral line nerves of the head and trunk, and of the nerve to the auditory organ, the former being in close relation to the cerebellar crest, the latter lying more ventral. There is no evident separation of the nerve to the auditory organ into a cochlear and a vestibular root.

The cells of the eighth nucleus. The cerebellar crest of the eighth nucleus contains cells precisely similar to those of the molecular layer of the cerebellum, with which it is continuous, and placed along the ventral aspect are the Purkinje's cells. Schaper has pointed out that the Purkinje cells of the selachian cerebellum are less well-developed, and less characteristic, i.e., have fewer and less regularly arranged processes than the Purkinje's cells in the cerebellum of other vertebrates.

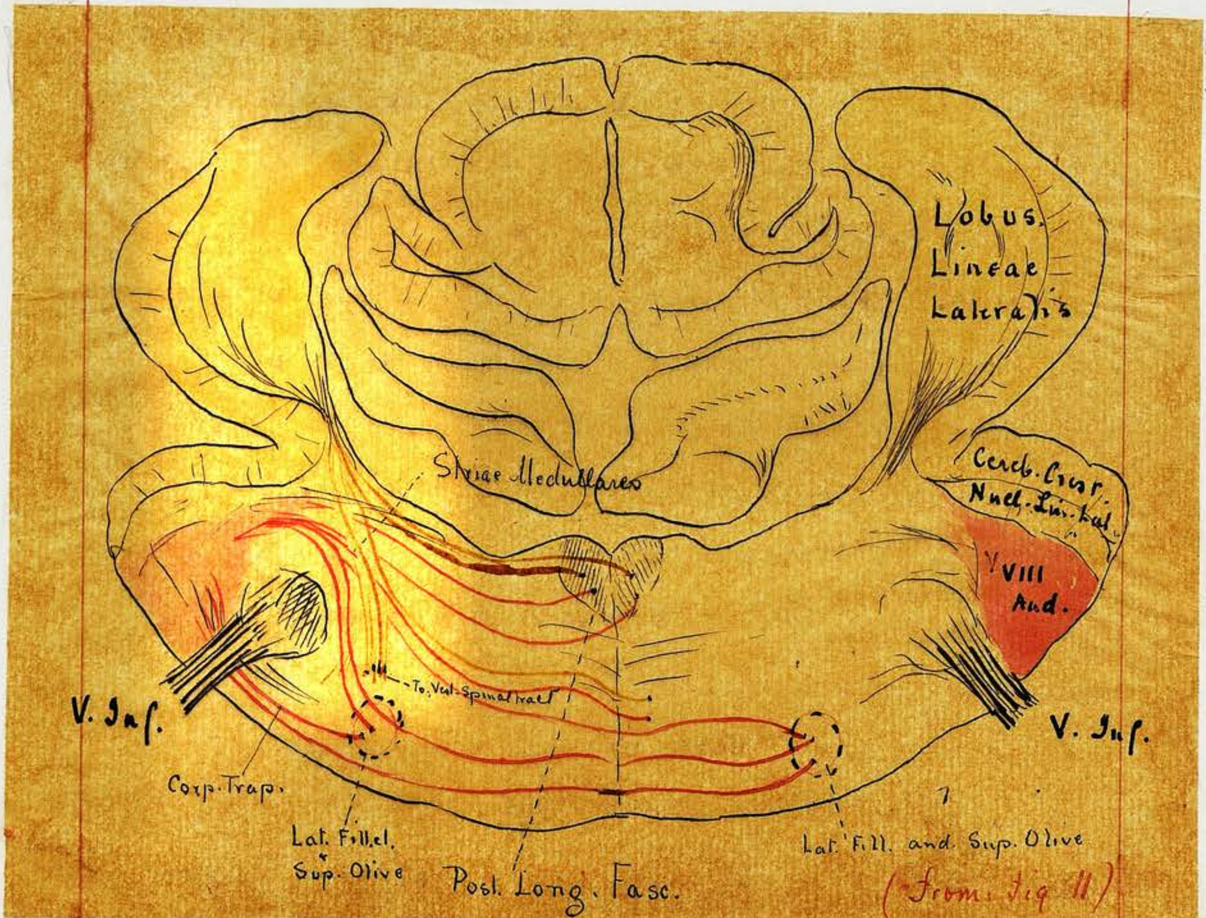
Scattered among the groups of fibres of the eighth nucleus are a number of small cells of varying shapes whose neurones turned forwards and joined the arcuate system in the manner described below. There are also some larger cells in the ventral portion of the nucleus which would correspond to Deiters' nucleus.

The Secondary connections of the eighth nerve.

The intra-cerebral secondary connections of the eighth nerve are probably simple, but the great number of fibres in the substantia reticularis renders it difficult to follow the individual strands. From the lowest to the highest portion of the nucleus fibres are given off which pass ventrally and become arcuate fibres. In their origin three sets of these fibres may be distinguished, a strong bundle from the superior lateral line nucleus: a group of fibres passing from the eighth nucleus internal to the inferior fifth nerve, and some passing external to this root.

The bundle from the superior lateral line nucleus, spreads out in a fan-shaped fashion in the medulla (figs. 5 — 12.) and apparently sends some of its fibres to the posterior longitudinal fasciculus of the same and of the opposite side, and another strand to the antero-lateral column of the same side. The vertical course of these fibres cannot be traced by the Weigert Pal method, but it is probable that, like the corresponding tracts in other animals, some of the fibres ascend in the two posterior longitudinal fasciculi to the oculo-motot nuclei.

Transverse Section, Showing Probable paths from Eighth nucleus

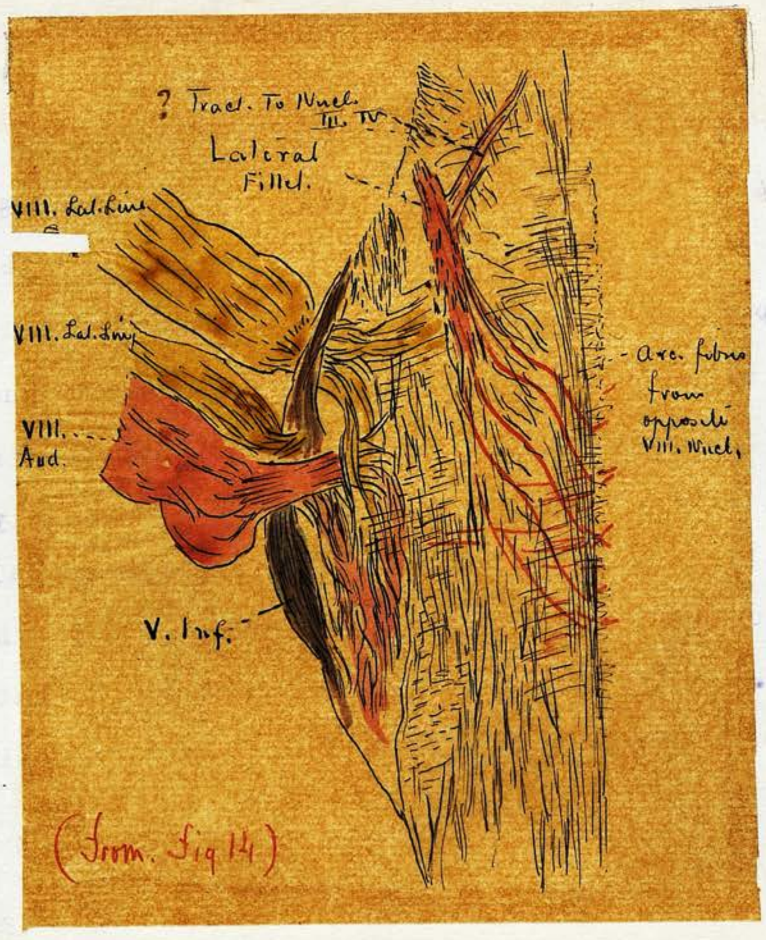


The difference in bulk which the posterior longitudinal fasciculus shows at this level proves that many others descend to the cord in this tract. The bundle which passes to the antero-lateral column would correspond to the vestibulo-spinal tract.

The arcuate fibres which arise from the eighth nucleus proper and pass internal to the inferior fifth root, are derived mainly from from the lateral line portion of the nucleus and have the same termination as the fibres just described.

Those which pass external to the inferior root of the fifth nerve, however, seem to terminate in part in the lateral region of the medulla of the same and of the opposite side. (Fig 12.). Longitudinal sections (Figures 13 & 14.) showed that they turned upwards and ended partly in relation to a nucleus at a higher level. (Fig). Some of the fibres passed still higher, to end in the lower part of the optic lobe. Some of the arcuate fibres which passed internal to the inferior nucleus of the fifth nerve, and crossed the raphe in its most dorsal portion, were seen to pass obliquely through the opposite formatio reticularis and also to end or bend upwards in the lateral part of the medulla. Their course strongly resembled that of fibres described by Kölliker in the human medulla as

Frontal Section Showing - Emergence of VIIIth roots -
" formation of lateral fillet



passing from one tuberculum acusticum to the opposite lateral fillet. These fibres, therefore, with the arcuate fibres which pass external to the inferior fifth root (<u>the corpus trapezoides</u>), bend upwards most probably into a structure analogous to the lateral fillet and nucleus, and would therefore constitute the centrally conducting path from the "auditory" portion proper of the eighth nerve of the skate. The more dorsal strand would represent the <u>striae medullares</u> and the more ventral strand the <u>corpus trapeziodeum</u> of higher vertebrates. The upper termination of this combined tract could not be acurately determined, but it ceased to appear as a definite tract at the lower part of the optic lobe, where there are several nuclei grouped together.

<u>Tract from the eighth nucleus to the oculo-motor</u> nucleus. In addition to these important tracts from the eighth nucleus another smaller one exists, which passes obliquely from the upper end of the eighth nucleus towards the oculo-motor nuclei (fig 13) ending partly in relation to the nuclei of the same side, and partly in relation to the opposite nuclei.

No evidence of the presence of Mauthner's large fibres could be obtained in the skate or in the shark. There was an isolated group of vertical fibres which extended upwards through the lower medulla and became lost about the level of the eighth nerve (Figs), but they were not in the position of Mauthner's fibres, nor could they be traced into any special connection with the eighth nerve.

It is interesting to compare the results obtained by the examination of the intra-cerebral course and connections of the eighth nerve of the elasmo-branchs with the description of the cranial nerves of this class given by Professor Ewart in 1889. He describes the facial nerve as a "facial complex" and rightly includes the superior lateral line nerve (the nerv. trigem. dorsal. II. of Goronowitsch in this complex, pointing out that its nucleus is only a "so-called" trigeminal nucleus. This branch, the buccal branch, and the hyo-mandibular, supply lateral line organs exclusively, while the palatine nerve supplies the spiracle and the roof of the mouth, and gives off a long slender nerve which he regards as the analogue of the chorda tympani. This nerve is derived from the fine-fibred root of the seventh nerve, which has just been shown above to be derived from the vagus nucleus. Ewart also recognised the independance of the lateral line nerves, and suggested their common centre. In a recent paper on Chimera, Cole describes the same relation of parts as in Laemargus and Raja, and the examination of a shark's medulla proved that the intra-cerebral parts were also alike. The observations of these authors tended to show that the so-called trig. dors. II was really a lateral line nerve, and that the whole lateral line system was an independent one, views which are fully borne out by the results of microscopic examination of the brains of the skate and shark.

Connections of the cerebellum.

No connection of the cerebellum with the cord directly were traced in the skate.

There was an extensive connection with the upper part of the eighth nucleus and the Uebergangs ganglion, which as already said is placed at the junction of the cerebellum with the medulla and acts as a centre for the ascending fibres of the fifth and eighth nerves; but no fibres were seen to pass directly from these nerves into the cerebellum. The fibres from the eighth nucleus curved upwards and backwards, those from the Uebergangs-ganglion passed directly backwards and radiated to all parts of the cerebellum; which in the skate shows a number of lobes.

A connection with the lower part of the mid-brain was made by means of fibres which passed out ventrally and slightly upwards, crossed the ascending tracts and were lost to sight in the lower and anterior portion of the mid-brain. Their mode of termination was not evident. They correspond to the "Bindearm" of German authors described in teleosteans.

Some fibres were also seen passing upwards from the cerebellum towards the optic lobes, but their termination was not determined. It should be noted that the valvula cerebelli was connected with the cord by means of a strand of very fine fibres passing upwards from the anterior column of the same side. These fine fibres ascend to the medulla from the cord, and continue in the anterior columns of the medulla. At about the level of the eighth nerve they bend backwards and pass obliquely towards the valvula cerebelli where they end.

The Eighth Nerve in the Teleost.

Plates. X— XV.

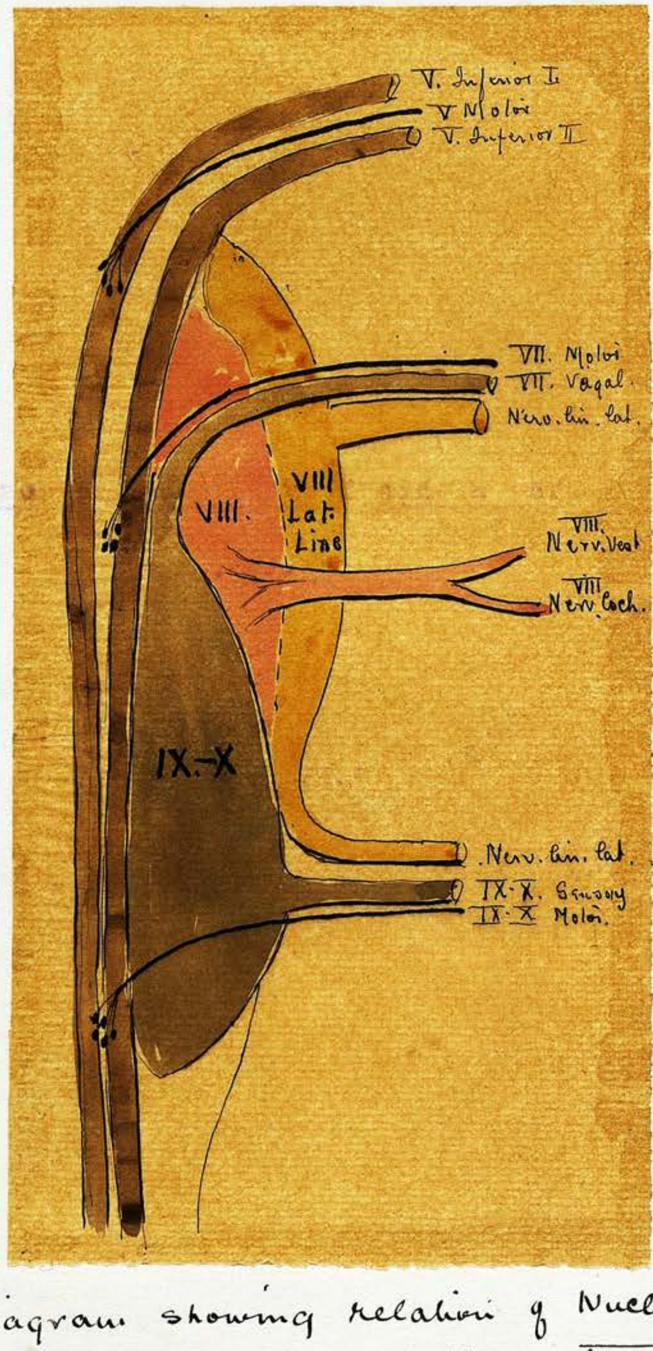
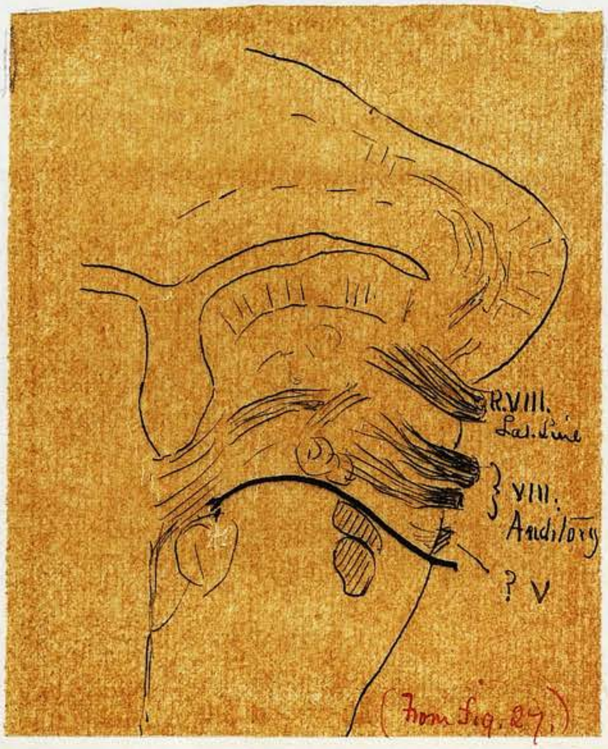


Diagram showing relation of Nuclei and Roots of. VII. VIII. IX. & X. in the Teleost.

The Eighth Nerve in the Teleosteans.

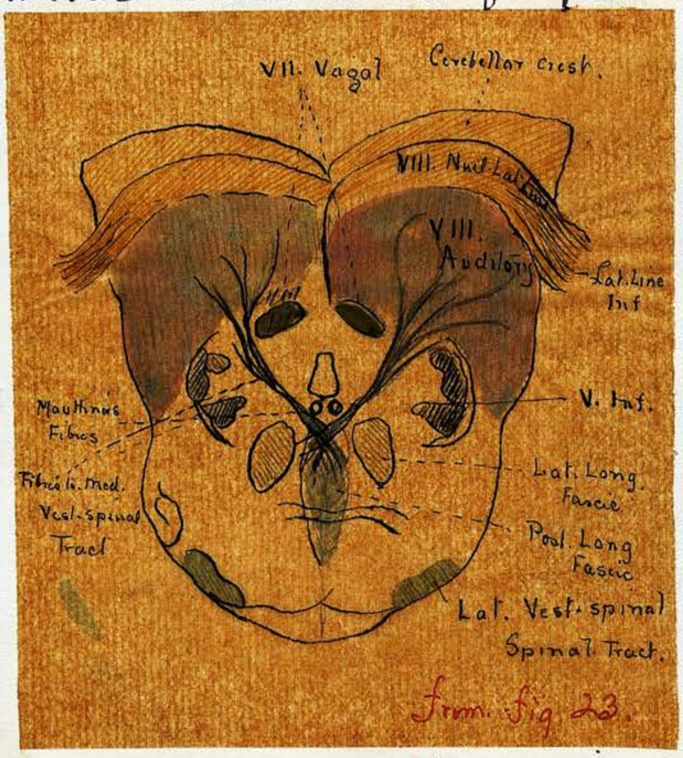
The medulla of the teleosteans is a most complicated structure, but the complexity varies greatly in different species. The specimens selected for illustration here were purposely chosen from the simpler types, since the complexity of the other forms is due to the extraordinary development of the vagal system, which greatly obscures the relationships of other parts. Reference to the results obtained by investigators of the teleostean medulla, however, showed that there was no fundamental difference in the arrangement of the various structures in different species, but that the apparent change was due to the great growth of the vagal lobe and the consequent displacement of neighbouring parts. It was therefore deemed advisable to select for this Thesis the simpler medullae in which the eighth system was not distorted or obscured by the preponderance of the vagal system. The fishes selected were the whiting, cod and common lythe (young) the last being the one figured here.

The teleostean medulla differs from the elasmobranch medulla in the greater complexity it shows, and further in the greater individualisation of its nuclei and tracts, which are much more sharply defined and therefore easier to follow.



Transverse section showing VIIIth roots emerging

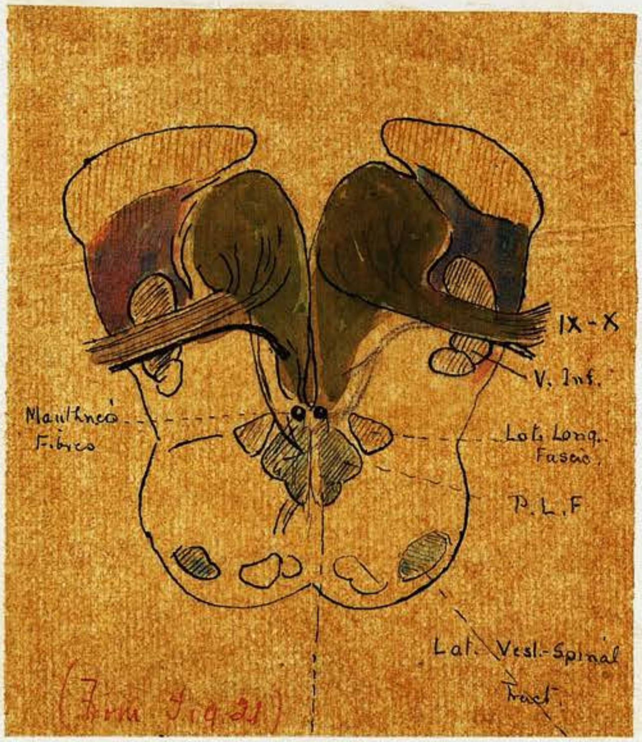
Transverse Section at level of inferior lateral line root of VIIIth



The eighth nerve in the teleostean is made up of the nerve to the auditory organ and the nerve to the lateral line (canal) sense organs of the head and trunk. The auditory nerve enters the medulla in two roots at least (fig.25.26), but there was not sufficient distinction between them to justify the use of the names cochlear and vestibular in relation to them. There was also a small root ending in the most lateral and ventral portion of the eighth nucleus which was closely associated with the upper part of the eighth root. The lateral line nerve enters also by two roots, one of which, the superior (Fig.25.26) supplies the canal sense organs of the head, the other, the inferior, (fig.23) those of the lateral line of the trunk. There is no lobus lineae lateralis in the bony fishes, and therefore no nerve corresponding to the nerve of this lobe. All the nerves to the lateral line organs end in the eighth nucleus. The auditory portion enters the ventral part of the nucleus, the lateral line portion terminates in the dorsal part of the nucleus. (Figs. 23-26)

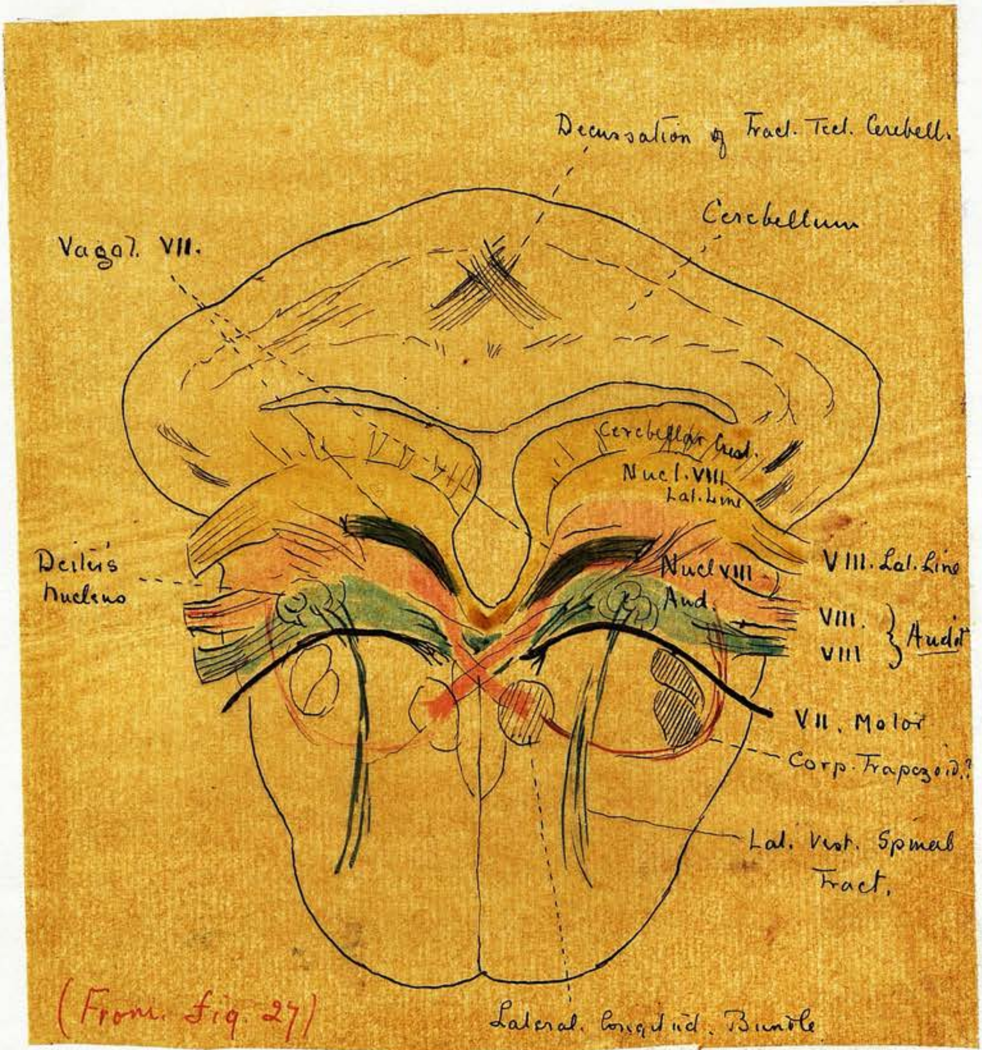
The fibres of these nerves divide on entering the medulla into ascending and descending branches, the division of the lateral line nerve taking place immediately on its entry into the medulla. The auditory nerves penetrate further, and many of them do not divide until they have passed some distance into their nucleus (figs. 25. 26). The descending branches of the auditory and lateral line nerves form the <u>inferior root</u> of the eighth nerve. This root passes downwards in the dorsal part of the medulla, lying dorsal to the inferior root of the fifth nerve, and the sensory nucleus of the vagus, and external to the nucleus of the vagus in its lower part. This latter structure though comparatively small in the fish from which the accompanying drawings were made, was still large enough to displace the inferior roots of the eighth and fifth nerves towards the lateral aspect of the medulla (figs 19-22). These descending branches or inferior roots of the eighth nerve, do not for the most part extend to any great length, but terminate, after a short course, in relation to the cells of the eighth nucleus, which is a much more circumscribed structure in the teleosts than in the elasmobranchs. The large vagus nucleus has pushed it outwards and backwards and has thus in a measure isolated it from the remainder of the medulla. A few fibres of the inferior root of the eighth nerve are continued

Transverse Section showing lat. eighth and vagal nuclei



downwards between the inferior root of the fifth nerve and the sensory vagus nucleus as far as the level of the lowest roots of the vagus nerve.

The eighth nucleus in the teleostean medulla, is placed on the dorsal aspect of the medulla and forms a definite, circumscribed nucleus with several nerves issuing from it. Its lowest appearance as a distinct nucleus is at the level of the upper vagus root, where it lies on the outer side of the vagus nucleus, dorsal to the emerging vagus root and inferior root of the fifth nerve (Fig. 21) It increases in size at higher levels, and, as the vagus nucleus grows smaller, the eighth nucleus gradually approaches the middle line, until it fuses with its fellow of the opposite side. In the specimens examined there was little more than a simple fusion, but in many teleosts there is a distinct commissural connection between the two nuclei. The nucleus is continued upwards, as far as the level of the fifth nerve, where it merges into another nucleus the "Uebergangsganglion" of Mayser, placed at the junction of cerebellum and medulla, some of the cells of the eighth nucleus form a distinct group or nucleus at the level of the seventh nerve, and give origin to the vestibulo-spinal tracts. This is the analogue of Deiters' nucleus. The



Transverse section showing nuclei of eighth nerve.

eighth nucleus may be divided into four different parts according to its structure:-

(a) A ventral portion.

(b) Deiters' nucleus.

(c) A median portion.

(d) A dorsal portion, or cerebellar crest.

(a) The <u>ventral portion</u> consists of a dense network of fibres containing many cells of varying sizes and shapes, but mainly multipolar. This part receives one of the roots (the saccular) of the auditory nerve. (Figs.21-26)

(b) <u>Deiters' nucleus</u> consists of large cells forming a definite group in the ventral inner and upper part of the nucleus, and receives the more ventral (vestibular) root of the auditory nerve. (Fig. 27)

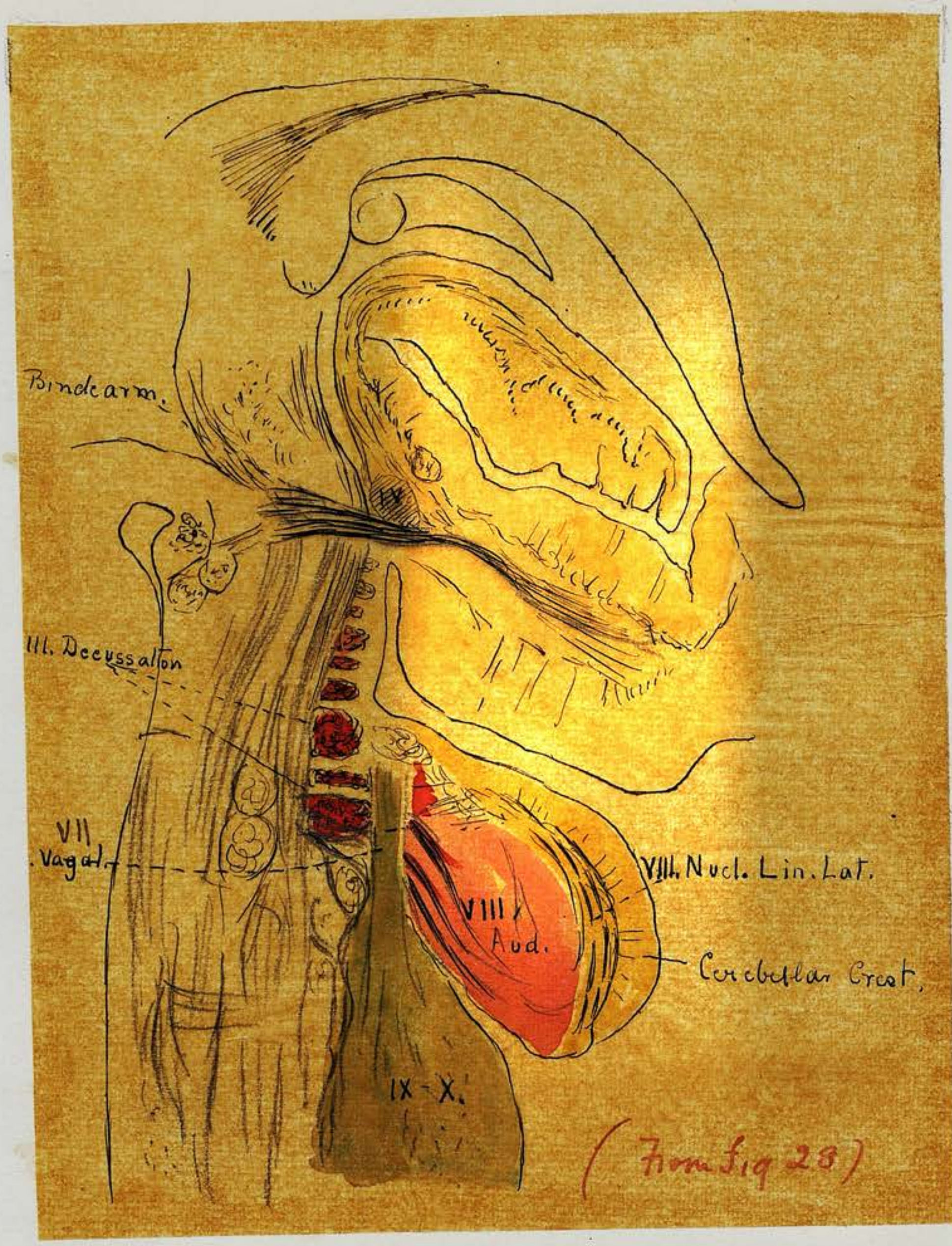
(c) The <u>median portion</u> of the nucleus consists of a much more open structure than the ventral portions, and contains many large cells within its meshes. The two lateral line nerves arise from this part. (Figs 23.25.26.

(d) <u>The dorsal portion or cerebellar crest</u>, consists of an extension over the eighth nucleus of the molecular layer of the cerebellum. On its ventral aspect are the characteristic Purkinje's cells, lying in close relation to the median, or lateral line part of the nucleus. This layer extends over the whole eighth nucleus and is directly continuous with the cortex of the cerebellum. (Fig 27.) It does not extend over the fifth or the vagus nuclei. On the ventro-lateral aspect of the eighth nucleus in teleosts there is an area paler than the rest of the nucleus which extends forward outside the inferior root of the fifth nerve, thus rendering this structure more deeply placed than in other vertebrates. This area gives rise to a nerve which emerges with the eighth nerve, but the exact nature and relationship of which is not clear. Mayser regards it as a branch of the fifth nerve.

The cells of the eighth nucleus.

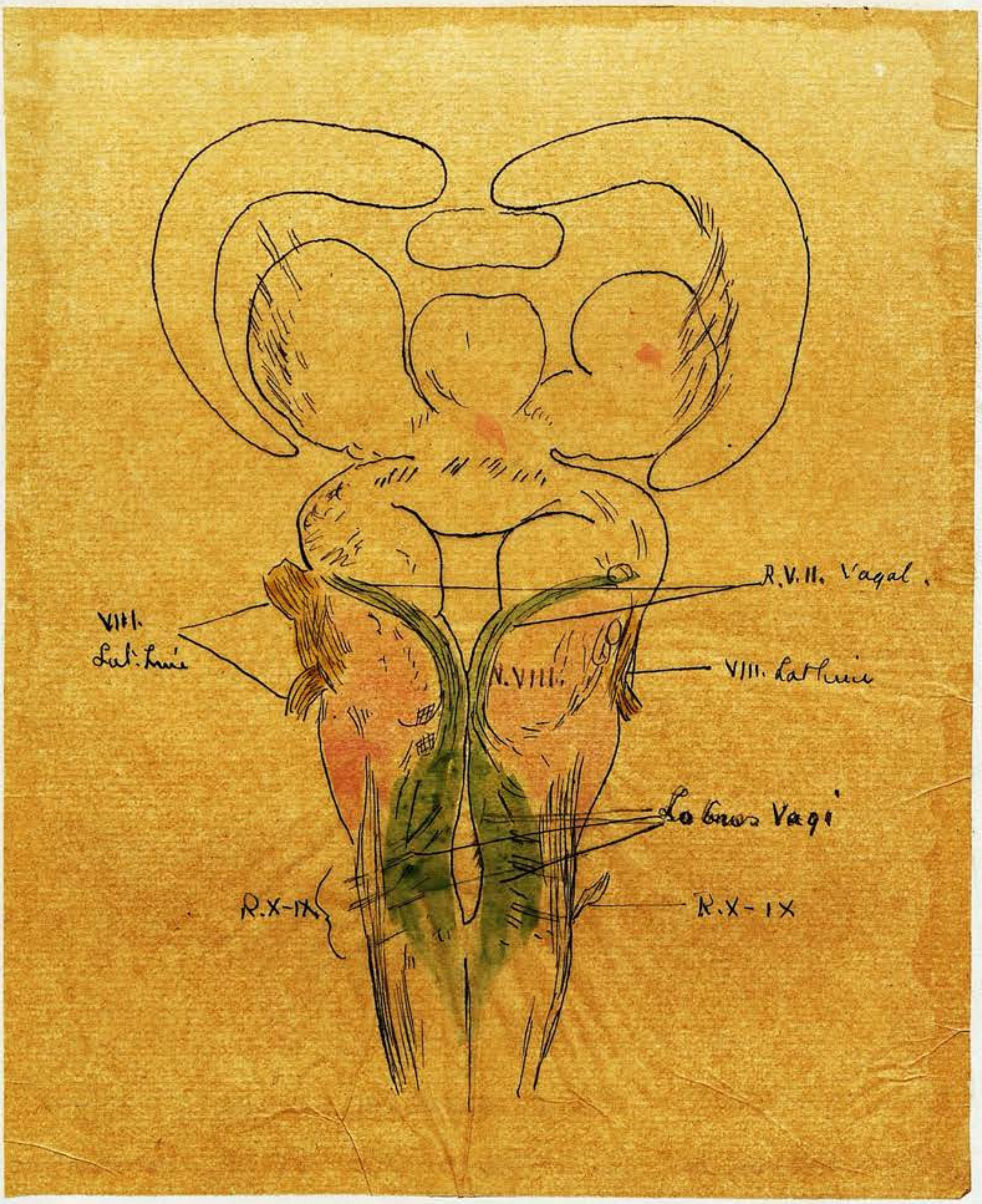
The cerebellar crest is composed of cells exactly similar to those of the molecular layers of the cerebellum, and along its ventral margin there are typical Purkinje's cells, more highly developed than those of the cerebellar crest in the elasmobranchs.

In the median and ventral part of the nucleus the cells are of all shapes and sizes. Some are large and rounded and resemble ill-formed Purkinje's cells, others are multipolar, both large and small. The cells of Deiters' nucleus are of the large multipolar type characteristic of this nucleus.



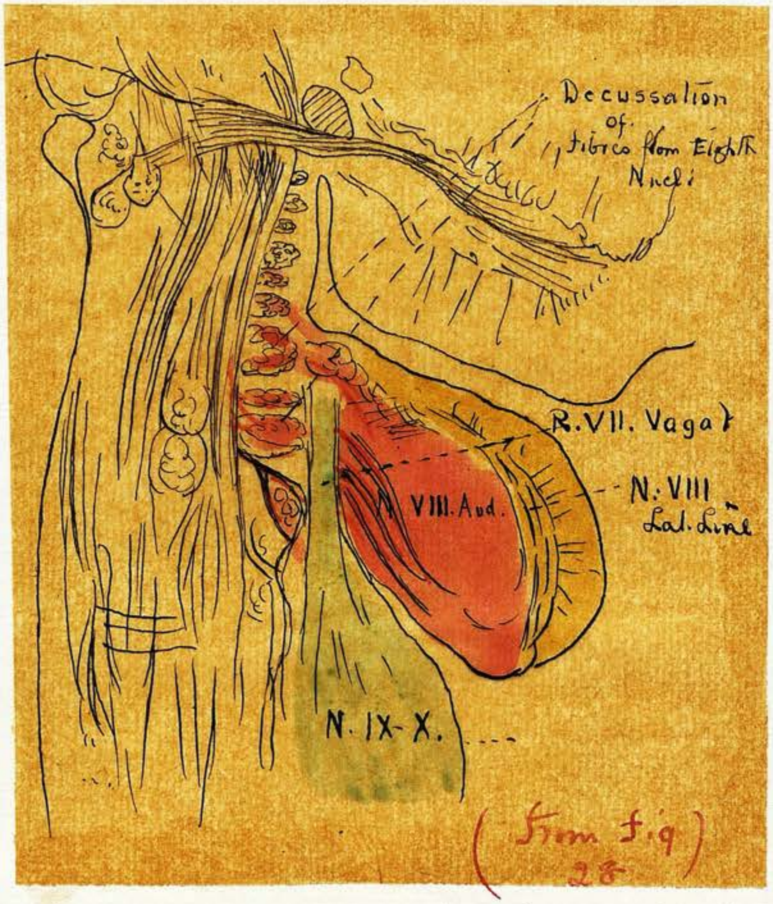
Sagittal section - showing relation of vagal and Eighth nuclei, and formation of vagal root of VII

The facial nerve in the teleostean medulla emerges in close proximity to the eighth nerve, as it does in the elasmobranchs and consists of two roots, a motor and a sensory. The motor ventral root is derived from a group of cells near the posterior longitudinal fasciculus (Fig 27), and the sensory (or vagal) root from the upper end of the vagus nucleus. Its course is best seen in the longitudinal sections (Figs. 28-32. and Fig. 33.) where it is shown to take origin from the upper pole of the vagus nucleus and pass upwards, ventral to the main part of the eighth nucleus and dorsal to the decussating bundles of fibres in this region. At the upper end of the eighth nucleus it bends outwards and emerges from the medulla dorsal to the emerging motor root of the seventh nerve (Figs. 27. 33). Mayser regarded it as a portion of the fifth nerve, but it is evidently the same nerve which emerged in immediate relation to the motor root of the facial nerve in the elasmobranchs, the only difference being that in the latter the ascending portion of the root was accompanied by a continuation of the grey matter of the vagus nucleus, whereas in the teleosts examined there is no grey matter. In other teleosteans, as is well known, the grey matter


R.V.II. Vagal.
VIII.
Lat. Line
N.VIII.
VIII. Lat. line
Lobus Vagi
R.X-IX
R.X-IX

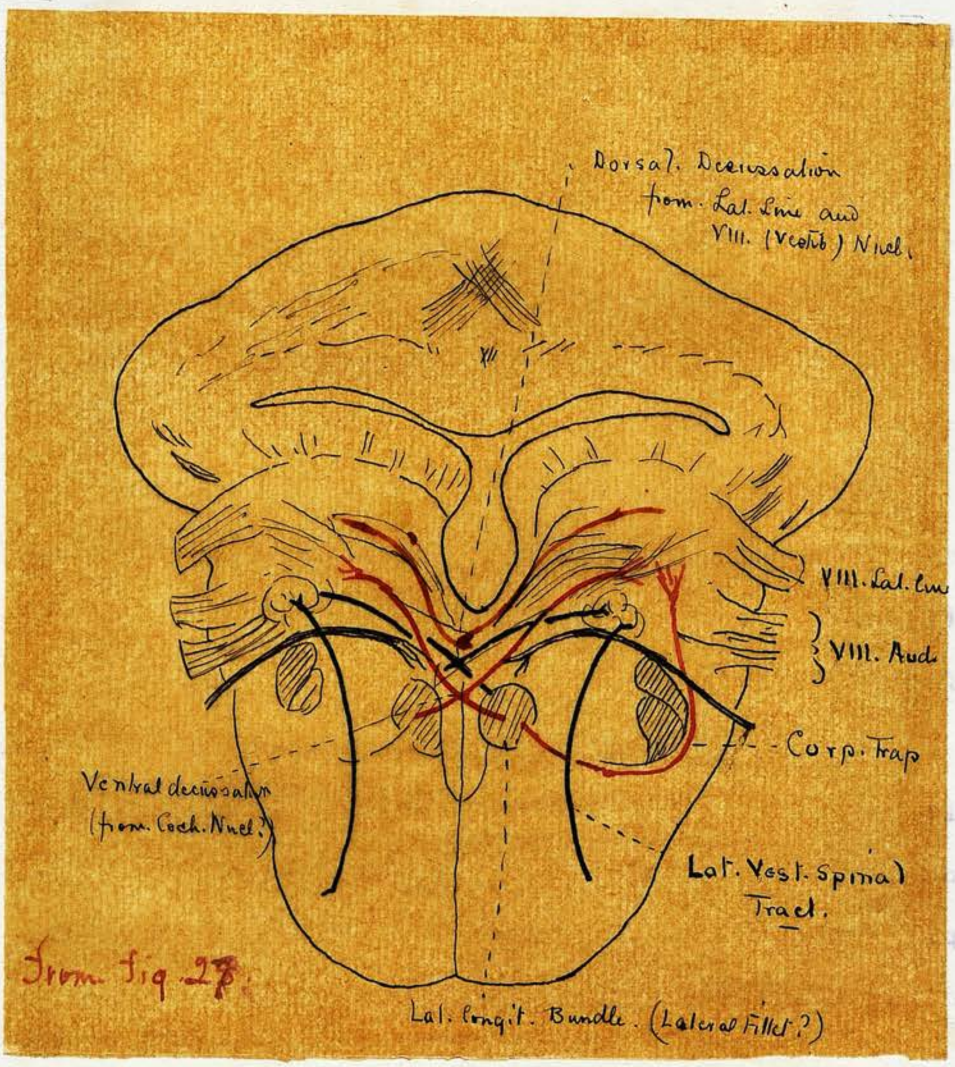
accompanying this root becomes so enormously developed as to form a lobe, which Mayser regarded as part of the fifth system and called <u>lobus trigeminus.</u> It is fully recognised, now however, that this lobus trigeminus is the greatly enlarged anterior portion of the vagus nucleus. The transverse sections (Figs. 23.- 25.) show the ascending portion of the nerve, and (Figs.26.27.33) its method of bending outwards and leaving the medulla.

As regards the emerging nerves of the VII - VIII complex, it will be seen that the only marked difference between the elasmobranchs and the teleosts is that the latter have no lobus lineae lateralis nor superior lateral line nerve, and that the vagal portion of the seventh nerve is further separated from its motor root in the teleosts than in the elasmobranchs. There is no doubt that the vagal roots of the facial nerve are the same however, and that they enter the palatine branch of the seventh nerve which gives off a branch analogous to the "chorda tympani" of higher vertebrates. Strong and Kingsbury both recognise the vagal lobe of the fishes as equivalent to the fasciculus communis of the frog, and Strong agrees with Kölliker that the fasciculus communis is homologous with the fasciculus solitarius in man. The examination of a series of vertebrate medullae leaves no doubt on this point. Its significance will be more fully explained later.



Sagittal section showing displacement of eighth nucleus by vagal nucleus.

The secondary connections of the eighth nerve, though in essentials similar to those of the elasmobranchs, differ in their arrangement, owing to the peculiarity in the development of the various structures in the teleostean medulla. The large lobus vagi pushes itself upwards and inwards between the eighth nucleus and the remainder of the medulla, in such a way that the latter is forced, as already said outwards and backwards, and is, to a certain extent, isolated from the remainder of the medulla (Figs. 28-32) The result of this arrangement is, that the fibres from the eighth nucleus to the arcuate system of the medulla instead of being given off throughout its longitudinal extent are gathered into thick strands within the nucleus, and after ascending to the level of the upper pole of the vagal nucleus (Figs. 28-29) pass inwards and forwards immediately below the floor of the fourth ventricle and decussate in the most dorsal part of the raphe (figs. 25-27). This well-marked decussation of the fibres from the eighth nerve is thus equivalent to the greater part of the arcuate system of the medullae of other vertebrates at the level of the eighth nuclei, and its presence explains the almost complete absence of an arcuate system in the teleost. A further result of this condensation of the arcuate

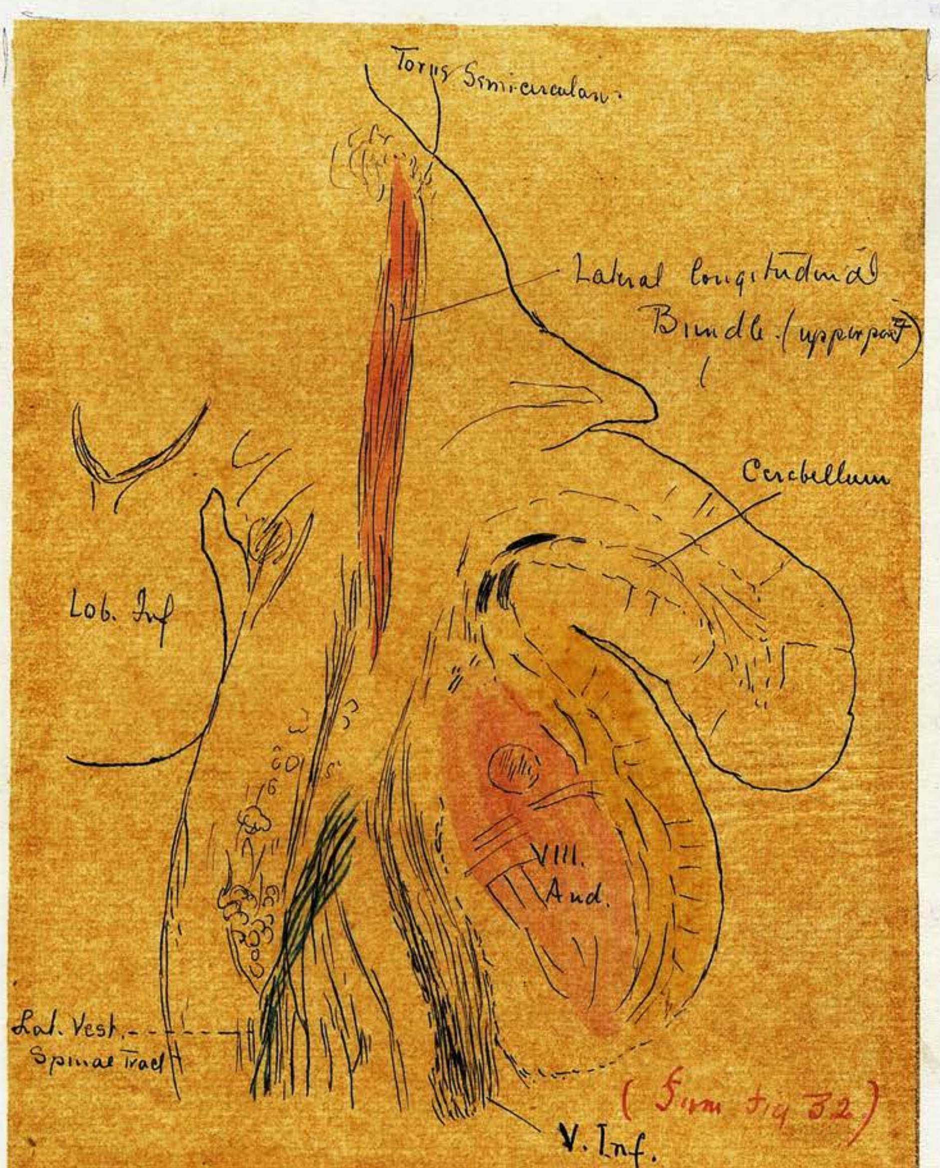


Transverse section showing connections of VIII^th^ nuclei system is that its main cerebral continuation, (the lateral longitudinal bundle of Mayser) which must be regarded as equivalent to the lateral fillet of other vertebrates, is situated much more dorsally and more deeply than in other forms, as will be seen below.

The fibres which form the main intra-cerebral connections of the eighth nucleus are, as said collected into distinct strands, and ascend within the nucleus, arching over the upper end of the vagal lobe, to emerge in dense strands from the ventral and most internal aspect of the nucleus. In addition to this strand a second relatively small group of fibres leaves the ventral aspect of the nucleus in its most external part, and curve round the outer surface of the inferior root. A third group of fibres, the lateral-vestibulo-spinal tract, leaves Deiters' nucleus to enter the lateral column of the medulla.

The first large strand of fibres is composed of two parts; of fibres which decussate more dorsally in the raphe and enter the posterior longitudinal fasciculus; (Fig. 26.) and of fibres which decussate more ventrally and enter the lateral longitudinal bundle. The former strand is coarser, arises in

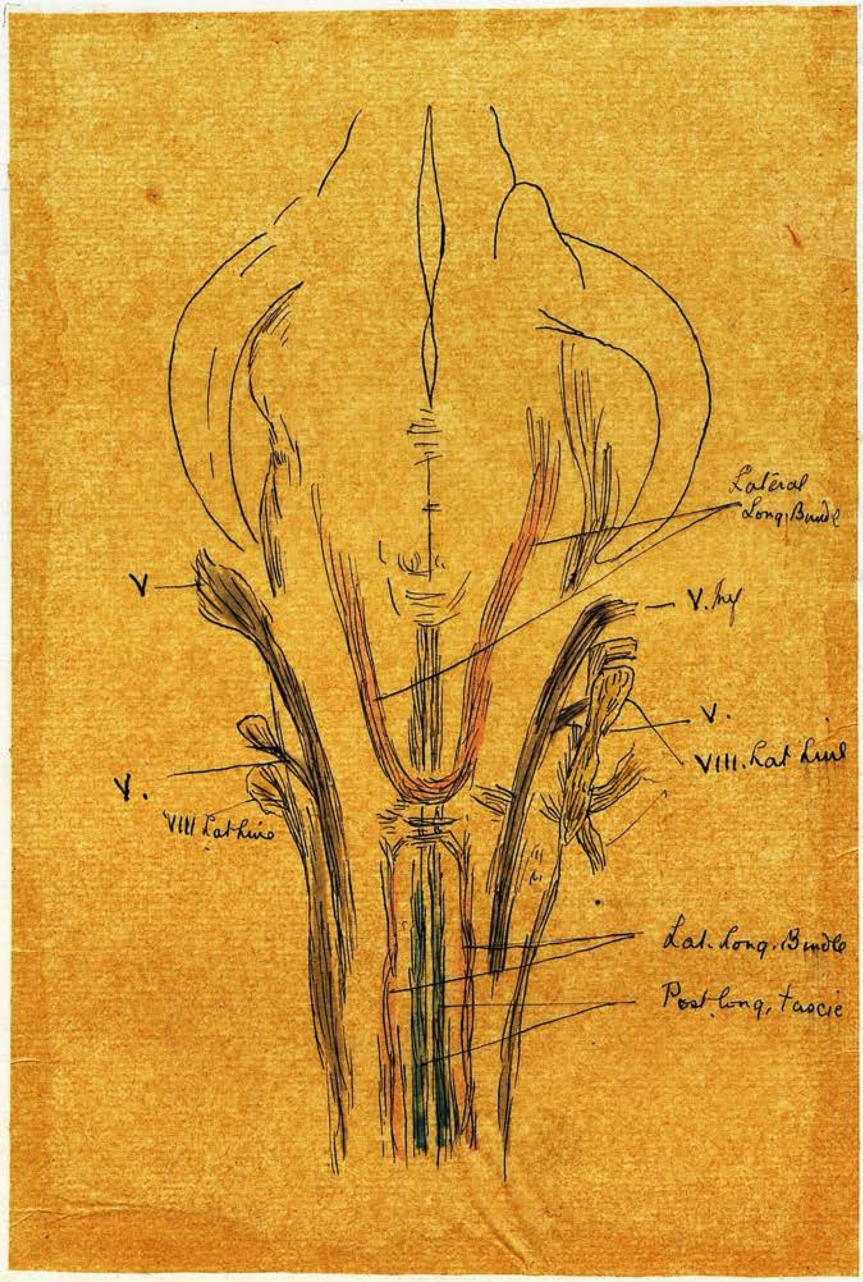
Sagittal section showing upper end of lateral longitudinal bundle.



(from fig 32)

relation to Deiters' nucleus, and will be included in the description of the strands from the nucleus. The strand which enters the lateral longitudinal bundle or lateral fillet decussates more ventrally in the raphe, crossing the fibres from Deiters' nucleus to the posterior longitudinal fasciculus in order to arrive at a more ventral position. (figs. 25.26.) Immediately after crossing the raphe, it turns upwards, joining or replacing a smaller strand of longitudinal fibres, which can be traced upwards from the lower medulla and cord to this level, (the lateralis Längsbundel) Figs. 34, 30.31.32, The upward continuation of this bundle is analogous as said above, to the lateral fillet. From the region of the eighth nerve the tract passes upwards, being accompanied in its course by irregular groups of large cells, most marked in its lower part. These cells would correspond to the superior olive and lateral fillet nucleus. The tract passes unaltered otherwise through the upper medulla, diverges somewhat from the middle line, and ends in the torus semi-circularis of the optic lobe, a nucleus which is probably represented by the posterior corpus quadrigeminum in mammals.

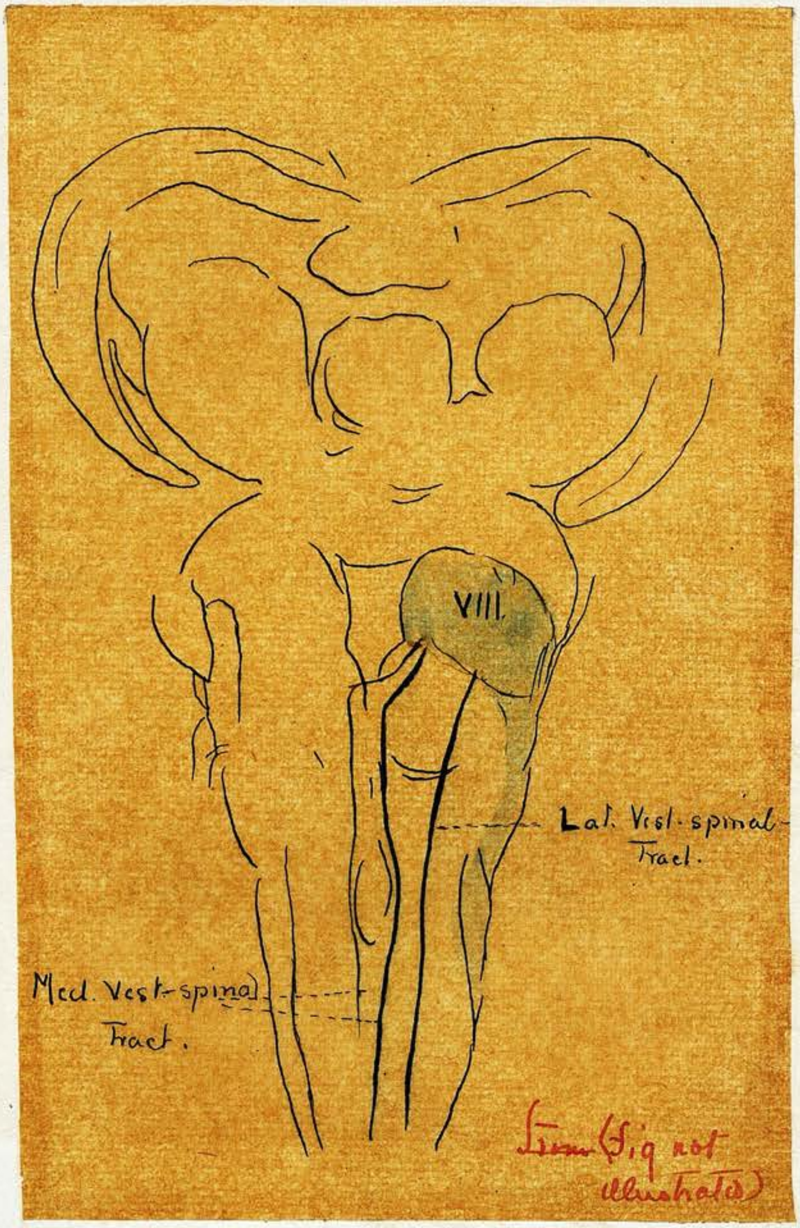
The second group of fibres emerges from the eighth nucleus on its lateral aspect and curves round the


Lateral Long. Bundl
V
V. Inf
V.
VIII. Lat Line
V.
VIII Lat Line
Lat. Long. Bundle
Post. long. fascic

inferior root of the fifth nerve (Fig. 25-26) to terminate in very close relation to this lateral longitudinal bundle, either by bending into the tract, or by breaking up among the numerous large nerve cells found in its immediate neighbourhood. The connections and arrangements of these two groups of fibres suggest that they are the equivalent of the central "acustic" path of the higher vertebrates, and that therefore the more internal group of fibres would correspond to the striae medullares the more external to the corpus trapezoideum while the lateral longitudinal bundle represents as said, the lateral fillet. This view is borne out by the fact that the whole of the arcuate system of this région of the medulla, which is entirely supplied by the eighth nerve, is evidently in close connection with this lateral tract, and further, that, except in the posterior longitudinal fasciculus, no other centrally conducting path upwards from the eighth nucleus could be found.

Connections of Deiters' nucleus.

The strand of coarse fibres which decussate in the most dorsal part of the raphe, (the median vestibulo-spinal tract) (figs. 27, 39) arises in the ventral part of the eighth nucleus from the large cells in this neighbourhood (Deiters'



Frontal Section showing connections of vestibular nucleus.

nucleus), and is evidently closely related to the more lateral fibres which rise from this nucleus and form the lateral vestibulo spinal tract. Ahlborn has described this system in petromyzon, and Mayser in teleosts, most fully and accurately; but both regarded it as a system which conducted centripetally, and which, in part, at least entered the eighth root and emerged as root fibres directly. They called it by the name of the original discoverer of these fibres, the system of Müllerian fibres. The more internal part of this system, the <u>median vestibulo-spinal tract</u>, arises from the internal aspect of Deiters' nucleus and passes towards the raphe; some of its fibres join the posterior longitudinal fasciculus of the same side and some enter the posterior longitudinal fasciculus of the opposite side. The researches of Mayser and others show that most of the fibres pass downwards towards the cord, but it is possible that some pass upwards towards the mid brain, as the posterior longitudinal fasciculus contains some of the characteristic coarse fibres as high as the level of the oculomotor nuclei.

<u>The lateral vestibulo-spinal tract</u> emerges from the ventral aspect of Deiters' nucleus (Fig.). Its

fibres are very coarse and may thus easily be traced. They pass inwards and forwards in bold curves, crossing the motor root of the seventh nerve. They then bend outwards to take up a position in the antero-lateral portion of the medulla (Figs. 29-30) where they assume a longitudinal direction and pass downwards throughout the lower medulla and cord, being distinctly distinguished throughout their course by their relatively large calibre.

These two tracts constitute in the fishes and frogs what was formerly known as the system of Müllerian fibres. Their analogy with the vestibulo-spinal tracts of higher vertebrates is beyond question, so that it is better to discard the old name, and give them the title which brings the system into line with other forms, viz., median and lateral vestibulo-spinal tracts.

There is a distinct strand of fibres connecting the eighth nucleus with the fifth nucleus (Fig 30), which terminated in relation to the cells of the latter nucleus, but its termination could not be definitely ascertained.

<u>The connections of the cerebellum.</u>

The cerebellum of teleosts is connected with the <u>mid-brain</u>, the <u>medulla</u> and possibly with the cord.

Its only connection with the cord seen in the sections examined, was the tract from the lateral portion of the medulla, although Edinger states that there is a marked restiform body in the teleosteans. The connection with the medulla is an extensive one. Fibres pass between the cerebellum and the nuclei of the eighth and fifth nerves, (figs. 26-27 28-32.) and numerous fibres connect it with the "Uebergangs ganglion." The connection of this latter ganglion is chiefly with the upper part of the cerebellum and with the valvula. There is no evidence to show in which direction these fibres conduct, but comparison with other forms suggests that they pass out from the cerebellum to these nuclei. No root fibres were traced from either the fifth or the eighth nerves directly into the cerebellum.

Two tracts connect the ventral and lateral columns of the medulla with the cerebellum.

1. A fine fibred tract rising from cells in the ventral portion of the opposite side of the medulla, passed round the periphery and entered the lower part of the cerebellum (Figs. 26-27 32.) Mayser describes it as rising from these cells and regards it as a cerebello-olivary tract. There are numerous

scattered cells throughout the ventral columns of the medulla, collected into little groups here and there and it is possible that they are the fore-runners of the inferior olive, in which case Mayser's view is correct.

The second <u>coarse-fibred</u> tract arises from cells and longitudinal fibres in the lateral part of the medulla, (Figs.23, 24.—27 & 32.) and passes dorsally in close relation to the fine-fibred tract, with which it enters the cerebellum. It represents the tract from the nucleus lateralis and possibly a direct tract from the cord to the cerebellum.

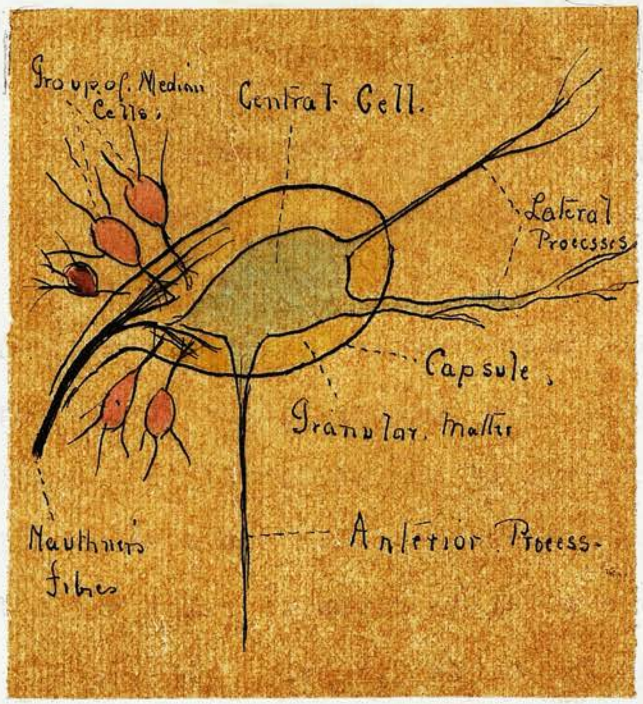
The cerebellum is connected with the <u>mid-brain</u> in teleosts by two distinct tracts (in addition to the tracts running between it and the lobus inferior)

The lower part is <u>coarse-fibred</u>, (Figs.28-29) and arises in all parts of the ~~medulla~~ Cerebellum. It forms a thick strand near the median plane of the cerebellum at its junction with the medulla, and passes ventrally and slightly upwards, external to the longitudinal fasciculus. It descussates dorsal to the third nucleus and ends in cells in this neighbourhood. This tract is known as the "Bindearm" by German authors, but its exact analogy with structures in higher vertebrates is not clear.

The second connection is a <u>fine-fibred</u> tract (Figs) which forms in the dorsal part of the cerebellum, and runs upwards and ventrally within it, somewhat external to the coarse-fibred tract. It decussates within the body of the cerebellum, then passes upwards to end in the mid-brain, near the torus semicircularis, at a higher level than the lateral longitudinal bundle (lateral fillet) from the eighth nucleus. The only tracts which can represent this structure in man, are the crossed fibres in the superior cerebellar peduncle which Russel traced across the vermis of the cerebellum into the opposite superior cerebellar peduncle after removal of the lateral lobe.

Mauthner's fibres. Figs. 18-25.

These remarkable fibres are present in most of the teleosteans. They are two giant fibres, or, rather, a strand of fibres enclosed in one medullary sheath, which are present in the most caudal extremity of the cord, pass upwards in its anterior columns without interruption, into the medulla. They are then situated in the dorsal part of the posterior longitudinal fasciculus within which they continue their course until they reach the level of the middle of the eighth nucleus where they decussate in the raphe and end in relation to a peculiar group of cells which form a special organ for these fibres. The most recent and complete description of these fibres is given by Kolster. He has proved by experiment that the fibres are centripetal, since they degenerate most markedly in their cephalic portion after division in any part of their course. They probably arise in cells at various levels of the cord, the fine fibres being collected into one common medullary sheath, within which they pass upwards towards the medulla, receiving fine fibrils at all levels throughout their course. At the level mentioned above, after the fibres have decussated, the medullary sheath disappears and the fibre breaks up into its

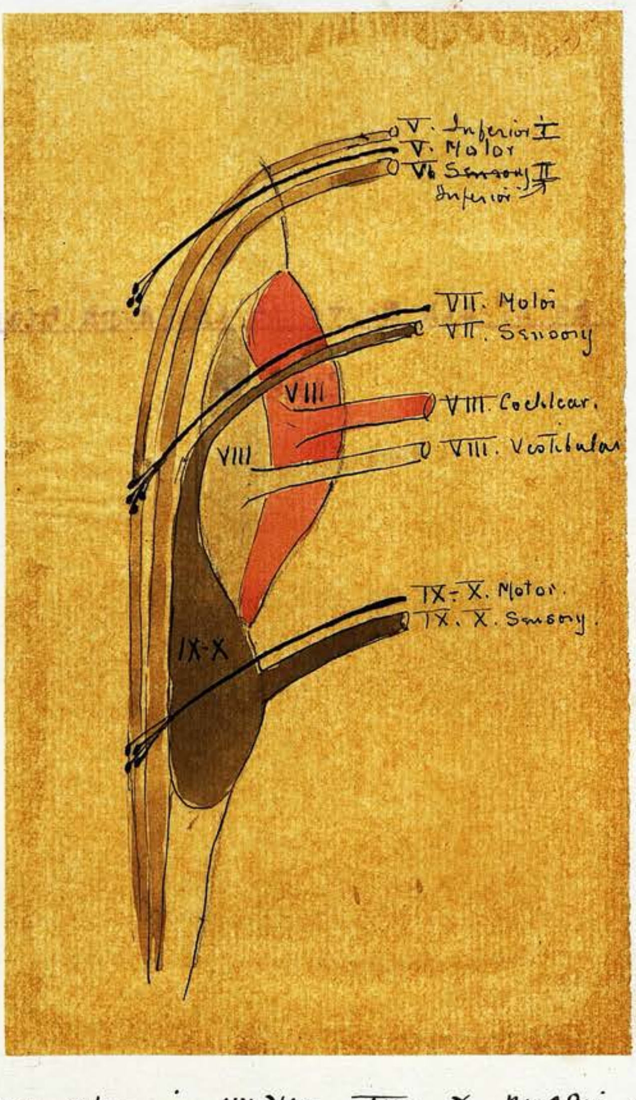


Diagram, showing end-organ of Mauthner's fibre according to Kolster's description component fibrils. The thickness of the fibre appears to vary at different levels. The end-organ of this fibre consists of a large pear-shaped cell, placed on the side of the raphe in the floor of the ventricle, the point directed forwards and inwards. Surrounding the cell is a layer of granular matter, within which the fibrils of the Mauthner's fibre ends, External to this layer again, is a capsule which narrows internally to a funnel-shaped opening, into which the fibre is received before it breaks up, and outside the capsule on the median aspect of the end organ there is a group of nerve cells whose processes end in the granular matter inside the capsule. The large central cell has processes which pass out ventrally and laterally, the lateral ones coming into relation with the eighth nucleus. There is one very large ventral process which passes directly ventral and then turns forward, giving off one or two small collaterals on its way. It probably is the axis-cylinder of the cell (Kolster), but its termination is unknown. Mauthner's fibres are present in most of the teleosts, in some of the ganoids, dipnoi, and in several amphibians. They are not present in any selachian cerebellum examined. Kolster thinks them analogous to the large Müller's fibres found in amphioxus and in the cyclostomes, but there is little doubt that the Müller's fibres are present in all fishes and amphibians whether Mauthner's fibres, are represented or not, as will be seen below. If Kolster's views are correct, it is evident that Mauthner's fibres with their end-organs must be part of the equilibrating system, forming a centripetal sensory path from all levels of the cord, which is in connection with the eighth nucleus and with some higher level as yet undetermined. It is generally believed now that the dendrites of a cell conduct centripetally, so that if the processes of the large central cell are ordinary dendrites, the cell must represent a centre where impulses which are derived from the eighth nucleus, and from various levels of the cord, meet, and are transmitted higher by the axone of the cell. It does not seem certain that this complicated organ is subject to the laws which control simple nerve cells, so all that can be definitely said at present is that it is part of a system peculiar to certain fishes and amphibians, which relates all levels of the cord with the eighth nucleus and possibly with higher parts.

These Mauthner's fibres are different from the coarse "Müller's fibres" which form the lateral and median vestibulo-spinal tracts. The former are the only survival of certain pairs of colossal cells present in ammocoetes (Mayer) and petromyzon (Ahlborn). In these forms there are several such pairs of cells, sending their processes into the cord by way of the posterior fasciculus, the most important being in the neighbourhood of the posterior commissure, the oculo-motor nuclei, and the eighth nuclei respectively. The only representative of these colossal cells and fibres in the higher fishes are "Mauthner's" fibres and cells, which appear, as just described, in the neighbourhood of the eighth nucleus. Mayer is of opinion that these cells and fibres are represented in the higher forms by groups of cells, forming nuclei and the strands of fibres known as Müller's fibres, but this seems improbable, since in some cyclostomes and fishes, and some amphibians, the two systems are both present, very fully developed. It is more probable that the colossal cells are peculiar to the lower vertebrates and disappear in higher forms, while the other system is permanent throughout the vertebrate series.

The Eighth Nerve in the Amphibian.

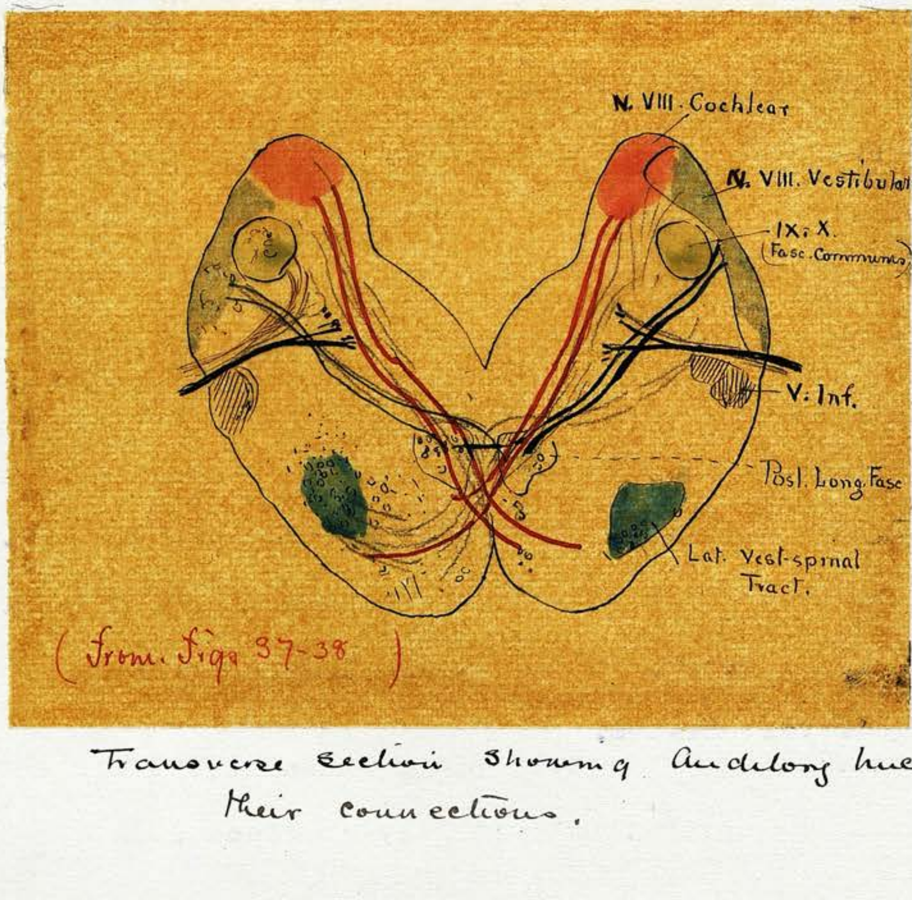
Plates. XVI – XIX.



Skeme showing VII. VIII. IX, X. nuclei and roots
in the frog.

The frog.

The medulla of the frog is much simpler in its arrangement than that of the fishes. Not only are the lateral line nerves and nuclei absent, but the remaining nuclei and tracts are clearly marked and comparatively simple, while the cerebellum is reduced to a mere transverse fold: The disappearance of the lateral line system is exceedingly well shown in the gradual transition of the frog from its aquatic to its terrestrial mode of life. Strong, who has studied the matter fully, proved that the tadpole possessed a set of dorsal sensory nerves which were unrepresented in the full-grown frog, and that these nerves supplied the lateral line sense organs, which are present in the tadpole at one stage of its growth, but which disappear when complete development is attained. Thus the seventh nerve in the tadpole consists of motor fibres and two varieties of sensory fibres, vagal and lateral line, but in the adult frog only the motor and vagal fibres are left; the lateral line contingent has disappeared. The tadpole thus resembles the fishes in the structure of its medulla in this respect, but the adult frog resembles the higher vertebrates.



Transverse Section showing Auditory Nuclei and ~~Nerves~~ their connections.

The eighth nucleus therefore in the tadpole supplies the auditory organ alone, and has no associated lateral line nucleus, and no cerebellar crest, which seems to be more peculiarly associated with the lateral line portion of the nucleus. The nerve might thus be correctly called the auditory nerve but regard being had to the double function of the inner ear it is perhaps wiser to adhere to the wider term "eighth nerve".

The first distinct indication of the division of the nerve into cochlear and vestibular roots appears in the frog, and the corresponding nuclei are more individualised than in the fish. The cochlear nucleus will be described first, as it is the most conspicuous part of the system. The lowest of its cells appear at the level of the highest motor root of the vago-glossopharyngeal nerve, and become grouped into a distinct nucleus on the dorso-lateral part of the medulla, internal to the fibres of the inferior root of the eighth (to be afterwards described). Fig. 37. It may be mentioned here that owing to the small size of the cerebellum, the fourth ventricle is narrow laterally and deep antero-posteriorly, and the eighth nucleus is therefore more dorsally placed than in animals in which the cerebellum is highly developed. A glance at the plates will explain this.

This nucleus attains its maximum size a little below the level of the motor root of the seventh nerve, and then decreases, having completely disappeared at the level of the motor root of the fifth nerve. Throughout its extent, it continues to occupy a position in the most dorsal part of the medulla, internal to the inferior root and dorsal to the vestibular nucleus of the eighth nerve. Figs 37-41 As will be mentioned later it gives rise to a distinct nerve, the <u>cochlear root</u> of the eighth nerve.

The <u>vestibular nucleus</u> is not so well defined as the cochlear, as its cells are scattered amongst many fibres, instead of being gathered into a compact nucleus. It lies ventral to the cochlear nucleus, and is bounded internally by the arcuate fibres which issue from the latter, and ventrally by the emerging motor root of the seventh nerve for part of its extent. Its lower extremity is not definitely marked off, as it begins simply as scattered cells among the fibres of the inferior root, and its upper extremity merges in the fifth nucleus and Uebergangsganglion without a clear line of separation. Figs. 40-41

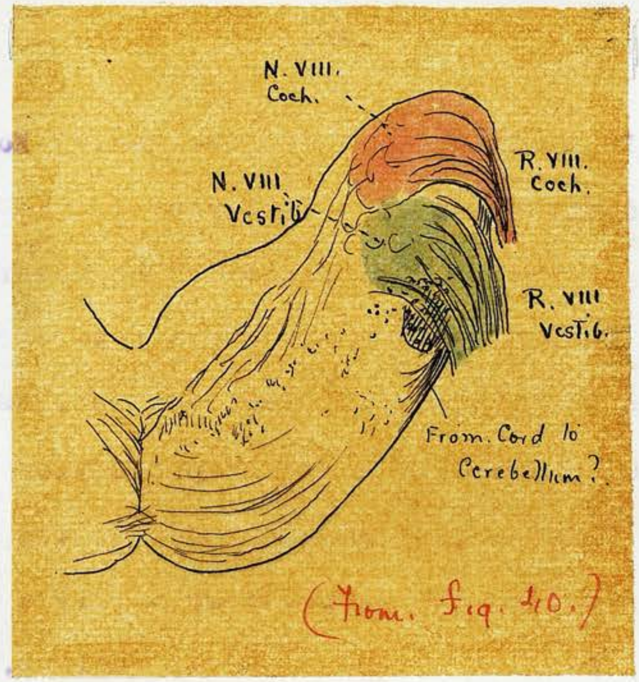
In addition to these two nuclei Köppen figures a small group of cells lying in the dorsal part of the cochlear nucleus, which he describes as a separate nucleus giving rise to a separate root. He compares it to a similar root and nucleus described as a part of the facial nerve in petromyzon by Ahlborn. This nucleus was not seen in any of the specimens examined and is probably merely a slightly specialised portion of the cochlear nucleus, or perhaps a vestige of the lateral line system.

The cells of the eighth nucleus.

The cells of the cochlear nucleus are large and rounded, while those of the vestibular nucleus are smaller and multipolar, with many processes. There were some large multipolar cells in its upper part representing Deiters' nucleus.

The roots of the eighth nerve in the frog are two in number, a dorsal or cochlear root and a ventral or vestibular root.

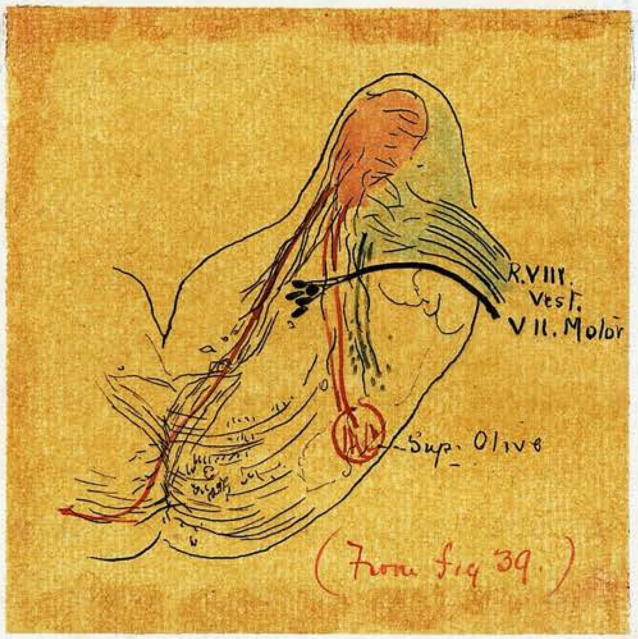
The cochlear root enters the dorsal or cochlear part of the eighth nucleus as a compact bundle of fibres which spread out within the nucleus in a fan-shaped manner, and terminates amongst the cells. It forms (Fig 40) a distinct single root whose fibres are distributed



Transverse Section showing cochlear and vestibular roots to the saccular sense-organs in the inner ear. The vestibular root, on the other hand, enters the medulla in scattered small bundles, piercing the dorsal part of the inferior root of the fifth nerve. (Fig 39-40.) Its fibres enter the vestibular nucleus, and break up into an ascending and a descending branch which end among the cells of the nucleus. The descending branches are strong and well-marked, forming the inferior root of the eighth nerve, but the ascending branches are shorter and feebler. They pass upwards, terminating at various levels in connection with the scattered cells in this region. These are related to both fifth and eighth nerves, and are probably analogous to the "Uebergangsganglion" of the fishes. The inferior root, as already said is composed of the descending branches of the vestibular root fibres. It contains among its bundles of fibres many cells, the downward continuation of the vestibular nucleus. The fibres of this root extend downwards in the medulla, as far as the upper termination of the dorsal columns of the cord, and throughout its extent it lies on the dorsal aspect of the inferior root of the fifth nerve. In its lower part it is bounded internally by the sensory vagus nucleus. Figs. 36-40.

The Seventh Nerve.

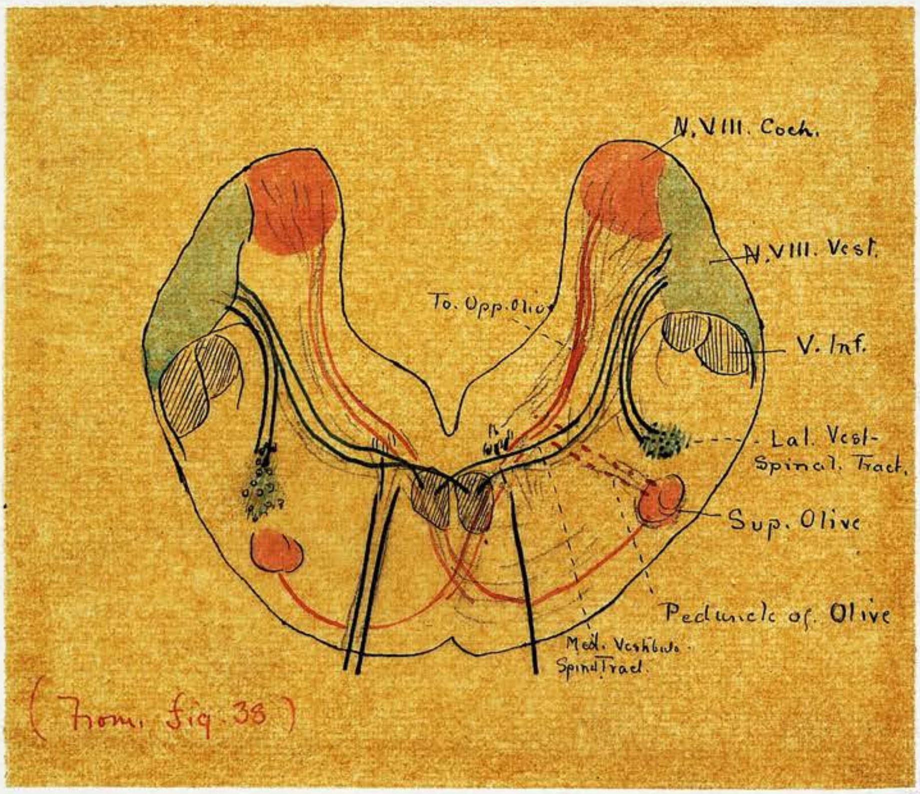
The seventh nerve in the frog consists of



Transverse section showing relation of motor root of VII. to the VIIIth (vestibular) nerve.

two roots, a ventral motor, and a dorsal sensory part. The ventral motor root, arises from a group of large cells lying ventral to the lateral angle of the fourth ventricle, further removed from the middle line than in the fishes. Fig. 39 It curves outwards, ventral to the vestibular nucleus of the eighth nerve, and emerges from the medulla in close association with the vestibular nerve. Fig. 49, 39.

The dorsal sensory root is the analogue of the vagal root of fishes - the pars intermedia of mammals. It arises from a very small upward continuation of the vagus nucleus, and emerges on the dorsal aspect of the motor root of the seventh nerve. It should be mentioned here, that the sensory vagus nucleus is much more restricted in size than it was in the fishes, and forms a small column of grey matter, (Figs. 51, 52) containing the ascending and descending branches of the upper sensory vagus roots which are collected into a definite tract known as the fasciculus communis in the lower vertebrates. The term fasciculus is unfortunate as in all cases there is more than nerve fibres in the column,—there are always associated cells forming a nucleus. The dorsal sensory root of the facial in the frog is derived from the upper end of this nucleus.



Scheme of connections of Cochlear and vestibular nuclei.

The connections of the Eighth nucleus.

Connections of the vestibular nucleus (Nucleus of Deiters).

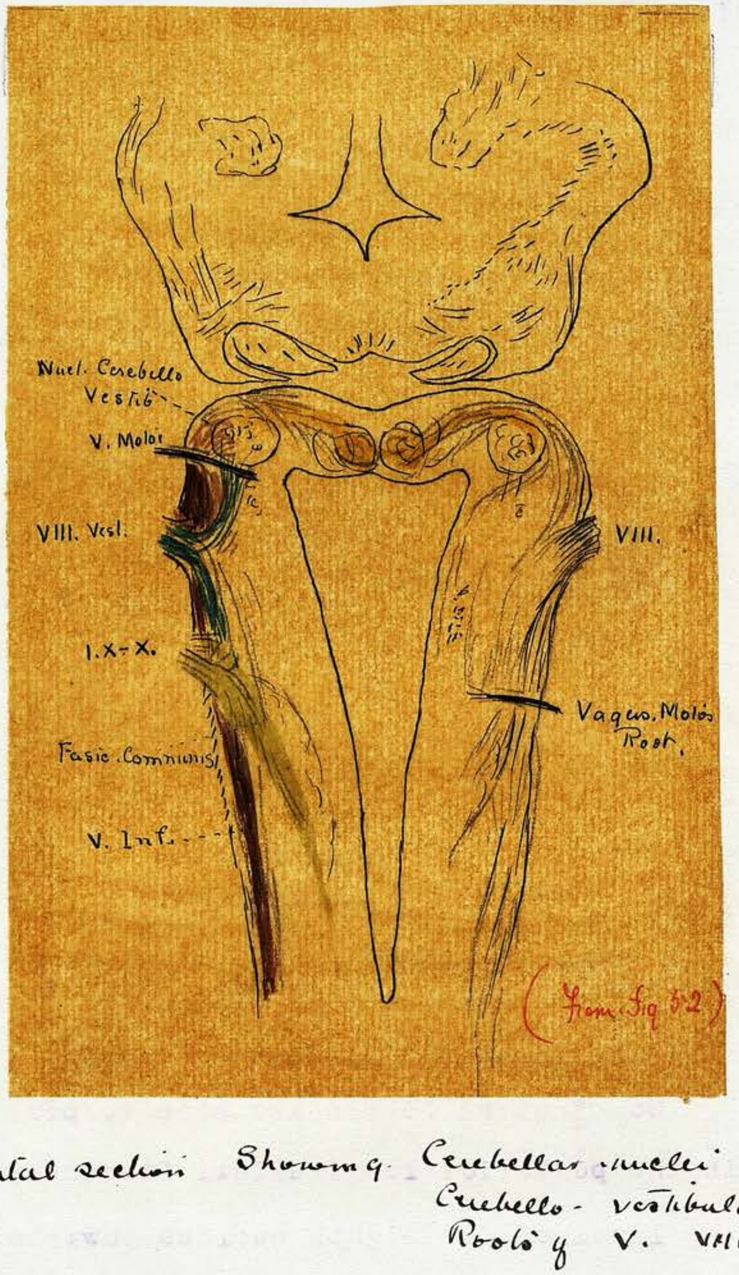
The more ventral portion of the eighth nucleus, that part which receives the vestibular nerve, has a very different intra-cerebral connection from the more dorsal or cochlear portion. The fibres which pass out from it are evidently divided into two sets, (Figs.). The first tract begins to emerge from it at the level of the upper vago-glosso-pharyngeal root, and extends upwards as far as the emerging facial root. The other tract is more limited in its origin, being only seen on transverse section, for a short distance above the level of the emerging facial root. These are the median and lateral vestibular tracts. The first tract emerges from the ventro-mesial aspect of the nucleus, and passes ventrally and inwards for a short distance, then turns more sharply inwards towards the posterior longitudinal fasciculus. (Figs. 35-38). Here some of the fibres remain while others cross the raphe to the fasciculus of the opposite side. The relative size of the fasciculus above and below this level, indicates that most of these fibres must turn downwards towards the cord.

The second set of fibres from the vestibular nucleus emerges also from the ventro-mesial aspect of the nucleus, but, as the fibres pass directly ventrally, they cross the first bundle at an acute angle (fig. 39) shortly after their emergence from the nucleus. They pass into the antero-lateral column of the medulla, where they also bend into a vertical direction and pass downwards towards the cord. (Fig. 39-40) The last described group of fibres is
f. 35-38 and 46.
easily distinguished by its open, loose character, and by the coarseness of its fibres.

Within the cord and medulla; the fibres from the vestibular nucleus are very prominent, when compared with the other fibres, by reason of their great size. They were fully described by Köppen in his article on the frog's brain, and were recognised by him as "Müllers fibres". Since, however, this term has been applied rather vaguely, and is often confused with the term Mauthner's fibres, I propose to discardit altogether, and give the tracts from the vestibular nucleus to the cord the same names as have been applied to it in the mammalian brain,-the vestibulo-spinal tracts.

The cerebellar vestibular tract.

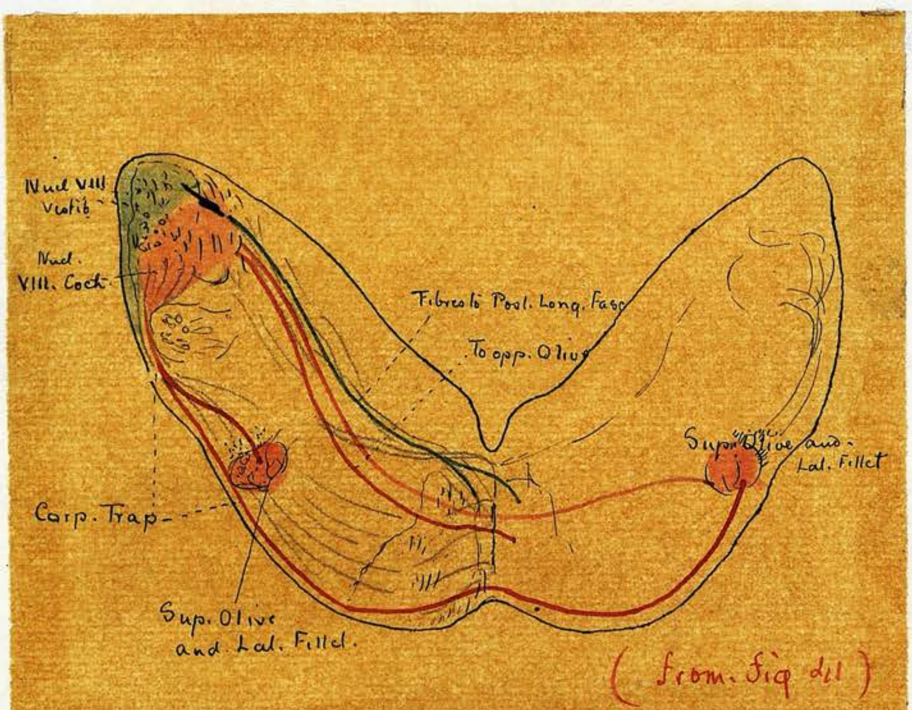
Some coarse fibres are seen to pass upwards in the posterior longitudinal fasciculus, above the level of the eighth nucleus towards the



Frontal section Showing Cerebellar nuclei
Cerebello-vestibular tract
Roots of V. VIII & IX-X.

mid-brain. These may be fibres from the vestibular nucleus to the third nerve, but I could not determine from the sections available whether they rose from this nucleus, or were continued upwards from lower parts. In the frog the fasciculus seemed to end almost entirely at the level of the third nucleus. (Figs. 44, 48)

In addition to these tracts, fibres are seen to arise in the upper part of the eighth nucleus and pass upwards towards the cerebellum. (Figs. 46.51.57). They were not direct continuations of the vestibular roots, but arose in the upper part of the nucleus. After passing upwards a short distance, they turned into a dorsal direction and spread out within a nucleus in the cerebellum, some of the fibres, at least, decussating to end in the opposite part of this nucleus. There is no evidence to show whether this tract is afferent or efferent to the cerebellum in the frog, but the natural inference is that it resembles the similar tract present in the higher vertebrates and undoubtedly efferent in their case. In these forms it is called <u>the cerebello-vestibular tract</u>, a term which I think may be safely applied to it in the frog also.

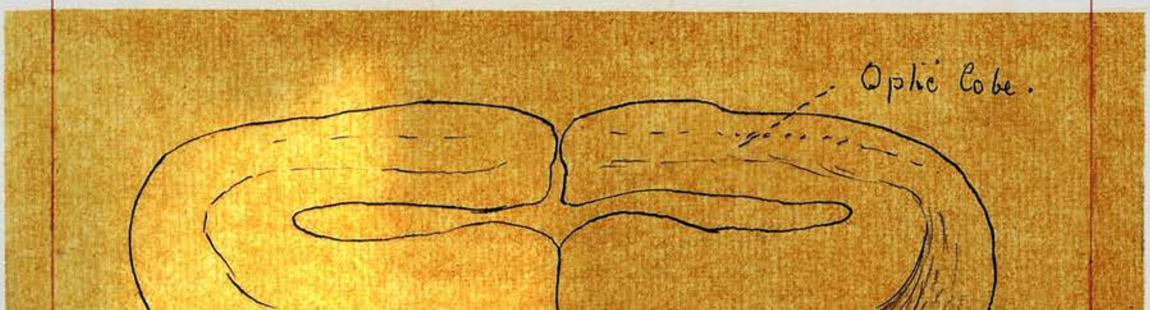


Scheme of connections of Cochlear nucleus

The connections of the cochlear nucleus.

From its lowest to its highest point (Figs 38-41) this nucleus gives off on its ventro-mesial aspect a large number of fine fibres, which become part of the internal arcuate system of the medulla; and in its upper portion it gives off a set of fibres passing external to the inferior root of the fifth nerve, which also become part of the arcuate system.

The first group of fibres passes forwards and inwards, crossing the bundle of fibres from the vestibular nucleus to the posterior longitudinal fasciculus, and is directed towards the raphe, which it crosses about the middle of its extent, ventral to the decussation of the bundle from the vestibular nucleus. Figs 38-41. Its fibres could not be traced further, but from the increase of fibres in the formatio reticularis at this level it is probable that some of them must have turned upwards. The remainder continue their course horizontally in the opposite formatio reticularis, running somewhat obliquely across it to terminate in relation to a nucleus, which, from its position and connections, is evidently the representative in the frog of the superior olive of higher vertebrates. (Figs. 38-40)



Transverse section showing termination of lateral fillet

This internal group of fibres from the cochlear nucleus would therefor correspond to the striae medullares. The second group of fibres from the cochlear nucleus curves outside the fifth nucleus as a compact strand, and then spreads out, fan-wise to form the more ventral portion of the arcuate system. (Figs. 40-41) The great majority of these fibres cross the raphe to the opposite side, where they either end in relation to the superior olive, or turn upwards without interruption, to form part of a tract which appears at this level. The group of fibres last described would thus correspond to the corpus trapezoideum of mammals, and the tract which turns upwards in relation to the superior olive to the lateral fillet. Traced upwards this tract is seen to form a distinct strand of fibres, gradually becoming more dorsally placed in the lateral region of the medulla and lower part of the mid-brain, until it reaches a level a little above the point of exit of the third nerve, where it bends backwards more sharply to terminate in relation to a nucleus in the lower and ventral portion of the optic lobe.(Fig. 44 45) This nucleus is the same structure as the torus semi-circularis of the bony fishes, and as Mayser pointed out, this structure is evidently the representative of the posterior corpus quadrigeminum of higher mammals.

I was not able to trace the upper termination of the tract from the cochlear nucleus which turned upwards in the formatio reticularis. It may be analogous to the tegmental tract described by Kölliker in the human medulla.

The connections of the Cerebellum.

The cerebellum of the frog is a very insignificant structure, and I could only find one strand (in addition to that connecting it with the vestibular nucleus), linking it to other parts. This second connection was a bundle of fibres which collected in the interior of the cerebellum and passed forwards and upwards after leaving it. (Fig 46) The fibres disappeared at the lower part of the optic lobe, but it was not possible to decide whether they ended in relation to the parts here or decussated and ended in the opposite side, too little was known about the tract to justify the application of the name superior cerebellar peduncle to it, although it resembled that body in some of its relations. There was no distinct evidence of a direct communication between the cerebellum and the cord, although Köppen mentions that the cerebellum receives tracts from the cord.

The valvula of the cerebellum was connected with the cord by means of tracts of fine fibres which ascended from the cord into the ventral columns of the medulla. At the level of the eighth nerve these turned obliquely backwards, lying externally to the lateral fillet, and appeared to terminate in the valvula. (Figs. 44.45). Similar fibres were described in the fishes.

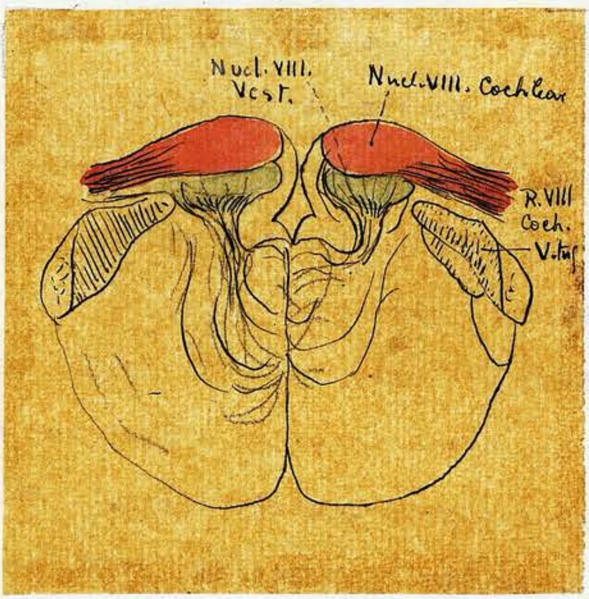
There were no Mauthner's fibres present in the frog, but Strong pictures them as present in the tadpole and in some amphibia.

The Eighth Nerve in the Reptile.

Plates. XX– XXII.

The Serpent.

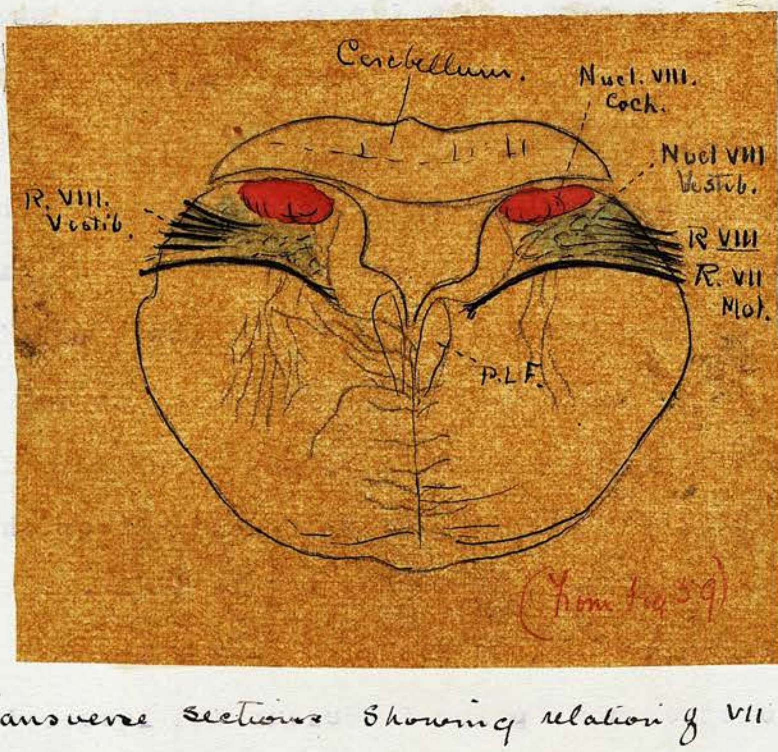
In some respects the reptilian medulla closely resembles the amphibian, the main difference being the closer approximation of the eighth nuclei, by the increased narrowing of the fourth ventricle, and the greater complexity and number of the strands of nerve fibres. As in the frog the cerebellum is small and insignificant, but the optic lobes are better developed and there is a distinct appearance of a posterior corpus quadrigeminum. The eighth nuclei lies, as has been already said, on the dorsal aspect of the medulla, even more markedly so than in the frog. It is distinctly divided into dorsal cochlear and a ventral vestibular portion of which the cochlear portion is the larger, and better developed, being more evidently a distinct nucleus in the serpent than in the fishes or the frog. The vestibular nucleus and its connections on the other hand are relatively small when compared with the corresponding system in other vertebrates. The relative importance of the cochlear nucleus and the posterior corpus quadrigeminum is to be explained by the great increase in importance of the sense organs of the reptilian cochlea. The want of development in the vestibular system is due evidently to the absence of any necessity for a complicated equilibrating mechanism.



Transverse section showing cochlear and vestibular nuclei.

The <u>cochlear nucleus</u> appears a short distance above the upper root of the vago-glossopharyngeal nerve. It forms an oval body, its long axis lying transversely with some fibres situated at its inner pole, and the cochlear nerve emerging from its outer pole. The nucleus is pale, and does not contain many fibres. It extends upqards almost as far as the level of the emerging fifth nerve, and attains its maximum size a little below the point of emergence of the seventh nerve. (Figs. 57-59). As in other forms the cochlear nucleus lies dorsal to the vestibular nucleus, which in the serpent, as already said is a comparatively inconspicuous structure. As will be seen from figure 59 , The cochlear nucleus is in close relation to the ventral surface of the cerebellum, owing to the displacement inwards of the whole eighth nucleus.

The <u>vestibular nucleus</u> lies ventral to the cochlear nucleus, and does not occupy so great a vertical extent as does the latter. In its lower portion (fig. 57-58) it appears on transverse section as scattered cells among strands of fibres, and is traversed by the arcuate fibres, some of which arise from the cochlear nucleus. At higher levels (figs. 59) the vestibular nucleus contains many cells and is therefore somewhat paler in colour and looser in



Transverse sections showing relation of VII and VIII (vestibular) nu texture than below. Its upper extremity merges insensibly into the lower end of the fifth nucleus and the Uebergangsganglion. It receives the fibres of the vestibular root, which break up within it into ascending and descending branches, (Fig. 65) the former terminating in relation to the cells at the upper end of the nucleus, the latter forming the inferior root.

The inferior root of the eighth nerve is formed by the descending branches of the fibres of the vestibular root. It lies dorsal and internal to the inferior root of the fifth nerve, and dorso-external to the sensory nucleus of the vago-glossopharyngeal nerve, where this is present. It extends downwards, its fibres gradually ending in relation to the cells scattered amongst them. The lowest fibres end in close proximity to the nucleus of the posterior columns of the cord. The inferior root of the eighth nerve is not so large in proportion to the remainder of the medulla in the serpent as in other vertebrates.

The seventh nerve.

The seventh nerve in the serpent as in the other vertebrates consists of a ventral motor and a dorsal sensory root.

The ventral motor root arises from cells placed

Transverse section, showing cochlear root.

somewhat laterally in the dorsal part of the formatio reticularis in much the same position as in the frog. Fig. 59 The nucleus did not appear to be so compact as in the frog and fishes, but consisted of more scattered cells.

The dorsal sensory root of the seventh nerve appeared on the dorsal aspect of the motor root, as a few fibres derived from the continuation upwards of the upper end of the sensory vagus nucleus. (Figs. 65.66). The sensory root of the vagus does not form a distinct fasciculus communis in the serpent, so that its nucleus resembles that of the fishes rather than that of the frog. There is a slight suggestion of the fasciculus solitarius in one part of the lower medulla. (Fig. 55)

The roots of the eighth nerve are not so distinctly divided as in the frog, but the distinction between the cochlear and the vestibular roots is present.

The cochlear root, begins to appear, a little above the highest glossopharyngeal root. It emerges from the outer pole of the cochlear nucleus as a compact bundle, lying dorsal to the inferior root of the fifth nerve. Its fibres enter the nucleus, among whose cells they appear to terminate at once.

The vestibular root appears at a higher level, and in its lower part is closely connected with the cochlear root (fig. 58.), but at the level of the facial nerve, above the exit of the cochlear root, the vestibular root forms an independent structure. Fig 59 It enters the medulla in several small rootlets, partly through and partly dorsal to the inferior root of the fifth nerve, and breaks up in relation to the cells of the vestibular nucleus into ascending and descending branches. These have already been described. (page 87)

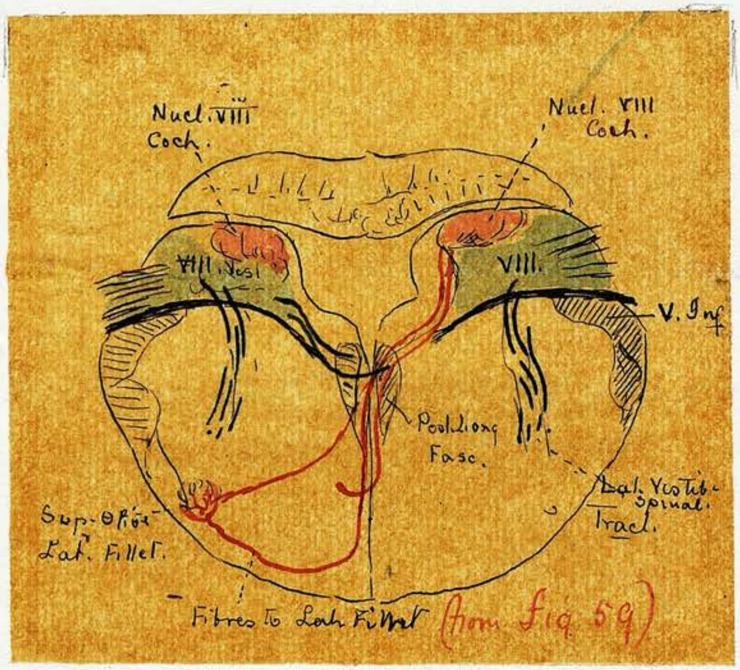
The cells of the eighth nucleus of the serpent are not described here, as the material available for the study of the reptilian medulla was very limited.

The connection of the eighth nuclei.

As in other forms described there are in the serpent two different paths from the eighth nuclei, a vestibular and a cochlear.

The vestibular nucleus gives rise to two sets of fibres, the median-vestibulo-spinal tract and the lateral vestibulo-spinal tract.

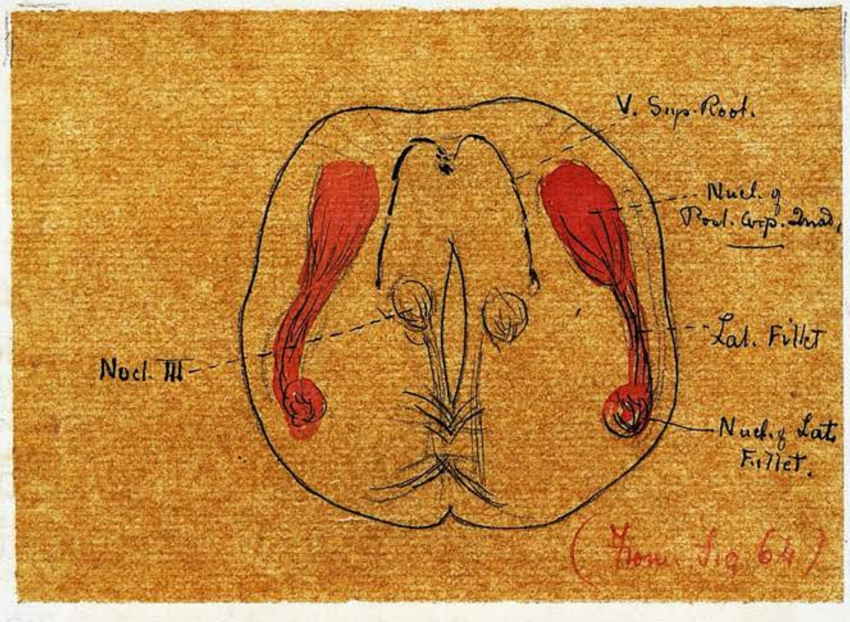
The median vestibulo-spinal tract arises on the inner aspect of the nucleus and curves forward towards the middle line, where in part, at least, it crosses the raphe. Figs. 56-59 Some of its fibres enter the



Transverse section showing connections of cochlear and vestibular nuclei.

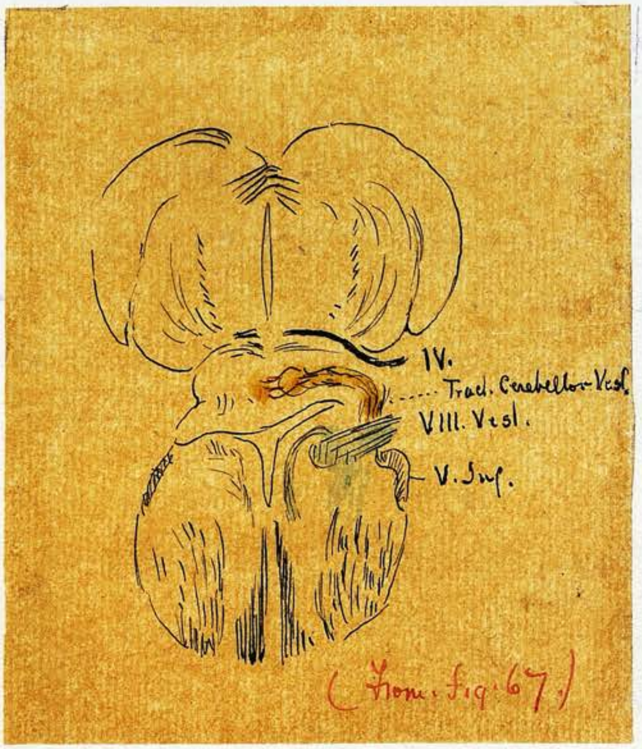
posterior longitudinal fasciculus of the same side, and some join the opposite fasciculus. Both these groups turn downwards in great part towards the cord. There is no doubt that the fibres of this system become incorporated to a great extent in the fasciculus; that they do not pass upward is evident since the fasciculus is smaller anove than below, so that the fibres entering at this level must pursue a downward path constituting the median vestibulo-spinal tract.

The lateral vestibulo spinal tract is much less conspicuous in the serpent than in the frog and the bony fishes. It arises from the ventral aspect of the vestibular nucleus, crosses the emerging root of the facial nerve as scattered fibres, and spreads out into a scanty, widely diffused tract, which, in transverse sections (Fig 59), traverses the medulla in a dorso-ventral direction, being also directed downwards, and is lost to sight in the formatio reticularis in the area dorsal to the superior olive. At this point it turns downwards and can be traced throughout the medulla as a group of coarse fibres, lying in the ventro-lateral column, from the remainder of which it is distinguished by the comparative coarseness of its fibres. (Figs. 53-58.)



Transverse section. showing lateral fillet and posterior corpus quadrigeminum

The cochlear nucleus is connected with other intra-cerebral structures by means of a broad band of fibres which emerge on its ventral aspect, traverse the vestibular nucleus, and enter the formatio reticularis as arcuate fibres. Some of these cross the raphe in its most dorsal part, others are more ventrally placed. Some of the more dorsally placed fibres continue their course obliquely across the opposite formatio reticularis and either end in relation to a group of cells there, the superior olive (Fig 58 & 16) or turn upwards, without interruption in this nucleus, to form a strand of fibres, the lateral fillet which passes obliquely upwards and backwards to end in the posterior corpus quadrigeminum. (Fig 64) The latter structure is well marked in the serpent, and contains a distinct nucleus, within which the fibres of the lateral fillet end. Others of these arcuate fibres run forward in the raphe to the most ventral portion of the medulla and then bend into the opposite antero-lateral columns where they end on the inner side of the superior olive, or pass upwards in the lateral fillet. Fig. 6.3 The fibres which approach the raphe in its middle third, are lost in the opposite formatio reticularis. All these arcuate fibres from the cochlear nucleus are the representatives of



Frontal section showing Cerebello-vestibular Tract.

the <u>striae medullares</u> of mammals. Fig. ~~57~~ 59. There were no arcuate fibres from the cochlear nucleus running externally to the inferior root of the fifth nerve so that there was no representative in the serpent of the corpus trapezoideum of mammals.

<u>The connections of the cerebellum.</u>

The cerebellum in the snake is a small and unimportant structure. It is connected with the eighth nucleus by the fibres which run from it to that nucleus. (Fig. 67) It has another tract which forms in its more lateral parts and passes into the medulla, at the level above the fifth nucleus. There it apparently becomes diffusely scattered, but some at least of its fibres decussate below the third nucleus (fig. 64). It may therefore be taken to represent the <u>superior cerebellar peduncle</u>; and is probably analogous to the "Bindearm" of the fishes. The upper portion of the cerebellum is connected with the cord by means of fibres which pass into it from the lateral portion of the medulla, the <u>corpus restiforme</u>, (fig. 61. 62), and the ~~valvula~~ Corpus ~~cerebelli~~ quadrigeminum, which is a large body in the serpent, receives fibres from the anterior columns. Fig. 62. These fibres pass up in the lateral and antero-lateral columns and begin to curve backwards along the periphery of the medulla into the cerebellum above the point of exit of the sensory fifth nerve. They continue to pass backwards throughout the whole extent of the valvula and lower part of the corpus quadrigeminum, the highest of the fibres being closely associated with the lateral fillet. Edinger figures them in the alligator and calls them tractus cerebello-spinalis The fine-fibres from the anterior columns have been described before as present also in the fishes and amphibians.

The Eighth Nerve in the Bird.

Plates. XXIII - XXVIII

The eighth nerve in the Pigeon.

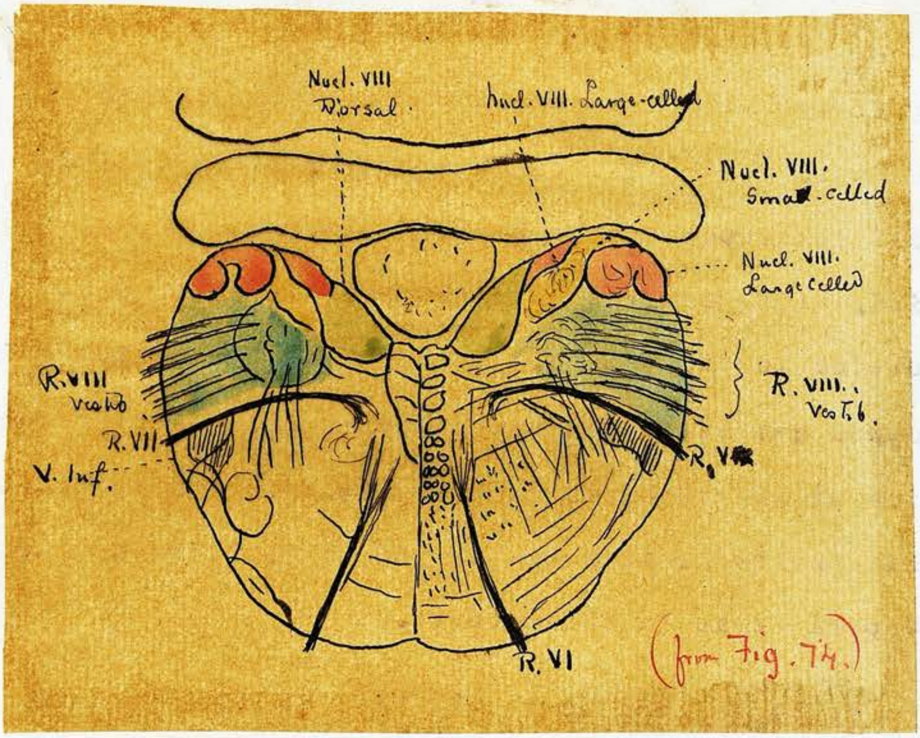
The medulla of the pigeon in many respects resembles that of the serpent in its general arrangement, as will be seen if the illustrated figures are compared. There are however some important differences, of which only those that relate to the subject at present under consideration, will be noted here.

There is a great increase in the size of the cerebellum, and the cerebellar nucleus has greatly developed, being now represented by two nuclei. The cochlear nucleus is somewhat increased in size and complexity, the vestibular root and nucleus are very much larger relatively to other parts than in any form as yet studied. There is no distinct corpus quadrigeminum. There is a distinct and important restiform body, conveying tracts from the cord to the cerebellum, and the inferior olives, which in lower forms were represented merely by scattered cells, now form ~~a~~ well-marked nuclei in connection with a system of arcuate fibres.

All these changes are evidently due to the great development of the necessity for equilibrating power in the life of the bird, and the greater complexity of the apparatus for hearing. It is interesting to note that in the bird the vestibular root is very much larger than the cochlear root, while in the serpent the reverse was found. The cochlear root is comparatively poorly represented in the bird, being smaller than in the serpent in proportion to the size of the medulla and the posterior corpus quadrigeminum has disappeared. The reduction of the cochlear root is explained by the fact that the cochlear sense organs of the bird are not so perfect as in the serpent.

<u>The cochlear nucleus</u> in the bird is divided into two parts which Brandis has described as a <u>large-celled nucleus</u>, the large-celled nucleus being in its turn divided into smaller groups by the passage of fibres through it, and a small-~~Allis~~ celled nucleus.

The lowest part of this nucleus appears above the level of the highest glossopharyngeal roots, (Fig 72.) and is placed on the dorsal aspect of the medulla external to the upper end of the sensory vagus nucleus and dorsal to the inferior roots of the eighth nerve. The large size of the sensory vagus nucleus in the pigeon pushes the cochlear nucleus in its lower part, somewhat further from the mesial plane than in the serpent. It appears at first as an oval group of cells on the dorsal aspect of the vestibular root, and gradually increases in size in higher sections until it has reached its maximum



Transverse section showing cochlear nuclei
emerging vestibular and seventh nerves.

a little below the level of the motor root of the seventh. It has also become displaced laterally by the development of a nucleus on its internal aspect (<u>the small-celled nucleus of Brandis</u>). This latter body is a long oval in shape, and is placed obliquely across the inner pole of the large-celled nucleus, in such a manner as to cut off a portion of the latter nucleus. (Fig. 74).) Its long axis runs forwards and inwards. It does not seem to receive root fibres directly, but only after their transmission through the large-celled nucleus. A few root fibres were seen to pass towards it, but were not traced into it. It is connected closely with the arcuate system, to which it contributes a great number of fibres. (Fig. 74, 87). The small group of cells cut off from the main large-celled nucleus by the development of the small-celled nucleus forms an upward extension, which appears at higher levels as a small oval nucleus in the lateral wall of the fourth nucleus, giving off some of the striae medullares. This nucleus has a close resemblance to the nucleus of mammals which Kolliker describes as being intimately connected in man with the striae acusticae.

Brandis has suggested that two of the subdivisions of the large-celled nucleus are the analogues of the anterior acustic nucleus and the tuberculum acusticum of mammals, but the position and relations of the various nuclei make it much more likely that the large-celled nucleus is the analogue of the anterior acustic nucleus, while the small-celled nucleus develops into the tuberculum acusticum. In support of this view it may be noted here that the corpus restiforme in birds passes into the cerebellum external to the cochlear nucleus, whereas in mammals it inserts itself between the cochlear and the vestibular nuclei, passing into the cerebellum on the inner aspect of the cochlear nuclei, which are thus displaced and made to assume a much more ventral and lateral position in mammals than in birds. If the figures illustrating the cat and the pigeon are compared, this will be evident (Figs 74. r Plate XXXI) By this alteration in position the small-celled nucleus(tuberculum acusticum) would come to lie on the dorsal instead of, on the internal aspect of the large-celled nucleus(the anterior acustic nucleus). This subject will be again discussed in the description of the mammalian cochlear connections(Page 152). It will only be mentioned here that the connections, and the character and arrangement of the cells of the two nuclei support this view.

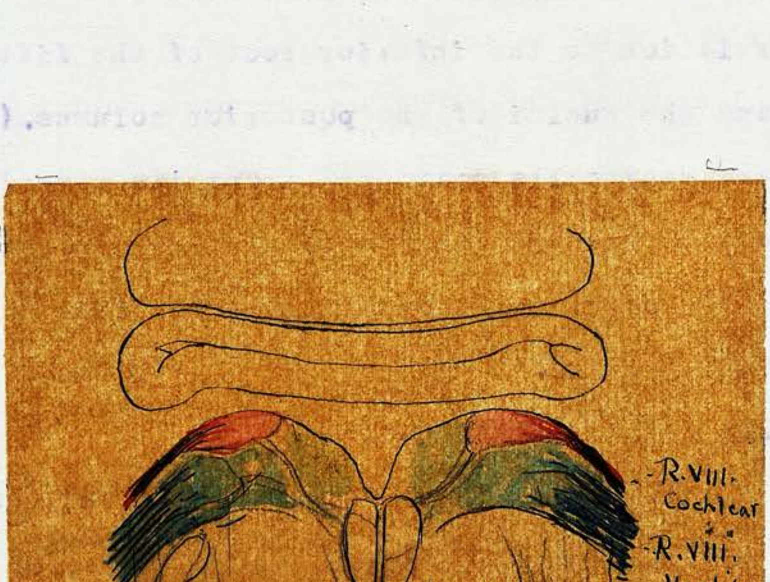
The vestibular nucleus in the pigeon as in other vertebrates is much less distinctly circumscribed than the cochlear nucleus. It consists of scattered cells lying among the inferior fibres of the root of the eighth nerve and, at higher levels, among the entering fibres of the vestibular root. At the level of the emerging root of the seventh nerve they are collected into a distinct nucleus (Deiters' nucleus) (Fig. 74.) which gives origin to the vestibulo-spinal tract. This group lies ventral to the small-celled cochlear nucleus. Its upper limit is not well marked, but is in connection with groups of cells which are present at the junction of the cerebellum with the medulla, scattered amongst the fibres of the various cerebellar tracts in this position. These scattered groups of cells merge into the proper nuclei of the cerebellum, (Figs 75-76 & 84) so that it cannot be said that there is a hard and fast line between these latter nuclei and that of the vestibular nerve.

The dorsal nucleus of the eighth nerve appears in birds on the inner side of the inferior root of the eighth nerve. (Figs. 74) Its lower limit is a little below the upper end of the vagus nucleus, and it extends upwards as far as the level of the upper vestibular roots. It consists of a number of small cells enclosed in a very fine network of fibres, which seem to be in part collaterals and in part the root fibres of the vestibular nerve. On its inner surface it gives off fibres which become part of the internal arcuate system.

<u>The inferior root of the eighth nerve</u> is formed by the descending branches of the vestibular nerve (fig. 67, and figs. 71. 72.) These pass downwards in the medulla in an area ventral to the cochlear nucleus, internal to the corpus restiforme and dorsal to the inferior root of the fifth nerve. The sensory vagus lies internal to it at lower levels. Its inferior limit is about the level of the hypoglossal nerve where it ends in close relation to the inferior root of the fifth nerve and the nuclei of the posterior columns. (Fig 70) There are many cells scattered among its strands, in relation to which the fibres terminate, so that the root is paler and less striking in birds than in many other animals.

<u>The cells of the eighth nucleus.</u>

The cells of the large-celled nucleus are large, some of them multipolar, but a number of them rounded and with few dendrites. The small-celled nucleus contains cells of various sizes, some multipolar, but mostly oval and all smaller than those of



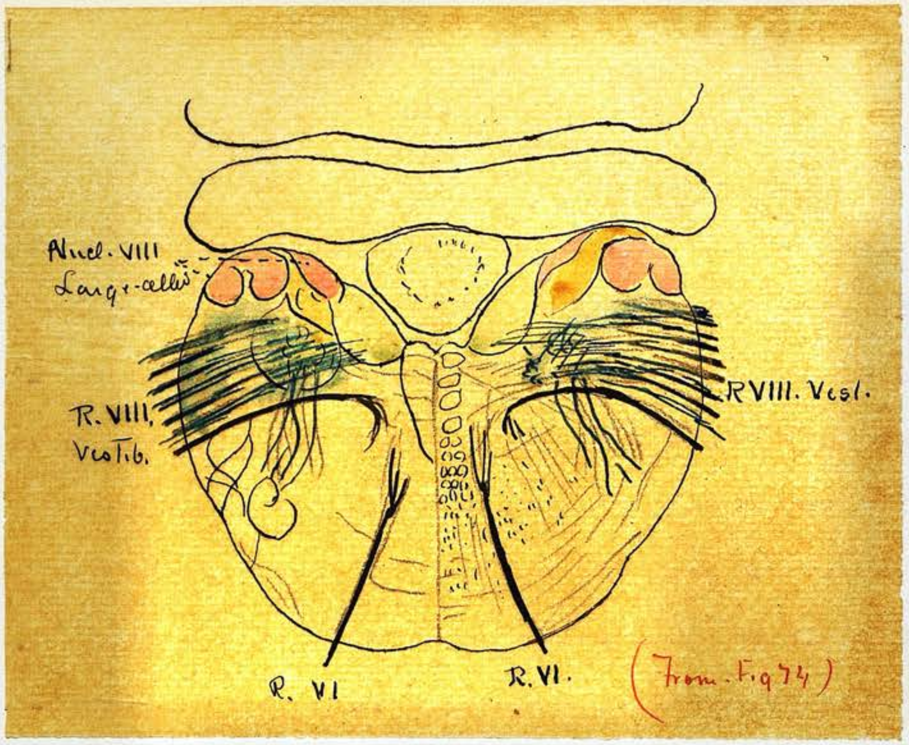
Transverse section, showing cochlear and vestibular roots.

the large-celled nucleus. They are arranged with their long axis lying at right angles to the long axis of the nucleus. The vestibular nucleus contains many cells of varying sizes but all multipolar. At its upper pole the group which gives rise to the vestibulo-spinal tracts (Deiters' nucleus) is formed of very large multipolar cells with many dendrites. The axis cylinder of the cells form the vestibulo-spinal tracts. Above the level of this nucleus are groups of irregularly scattered cells forming a large diffuse group the cerebello-vestibular nucleus of Brandis.

The roots of the eighth nucleus are two in number - cochlear and vestibular.

The cochlear root enters in one compact bundle dorsal to the inferior root and to the lower part of the vestibular root. (Fig 73) It breaks up immediately on entering the large-celled cochlear nucleus into fibres, which terminate in relation to the cells here, Some of the fibres seem to curve round the ventral aspect of the nucleus to enter the small-celled nucleus, but this appearance was not constant.

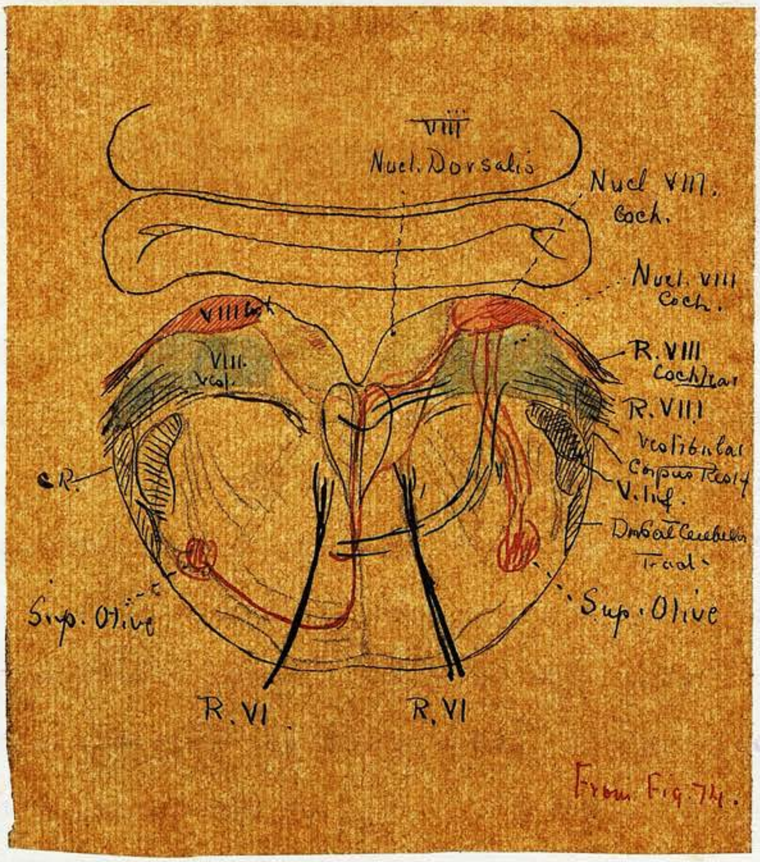
The vestibular root is very large. (Fig 74) It enters the medulla in numerous small bundles, piercing the restiform body. The lowest of these bundles breaks up into ascending and descending fibres very shortly



Transverse section showing vestibular and facial nerve roots after entering the medulla, but the higher bundle passes in considerably further to end in relation to Deiters' nucleus. (Fig. 74). Brandis states that these roots pass in as far as the raphe and cross the middle line, but apparently he has concluded that the roots are continuous with the great number of arcuate fibres which pass inwards from the whole vestibular nucleus towards the raphe.

The fibres of the vestibular root divide into ascending and descending branches, the former end in relation to Deiters' nucleus and the scattered cells forming the cerebello-vestibular nucleus. The descending branches, as already said, form the inferior root. The lower fibres of the vestibular root appear at the lower level of the sixth nerve, its upper fibres at the level of the facial nerve. It has a greater vertical extent than the cochlear root.

The facial nerve is apparently purely motor in the pigeon.(Fig 74)It arises from a nucleus in the formatio reticularis external to the sixth nucleus. There was no evidence in the sections examined of a pars intermedia, (a fasciculus communis or vagal root).



Scheme of connections of the cochlear nuclei.

The connections of the eighth nucleus are wide-spread in the pigeon, but show little or no variation from the conditions present in other types.

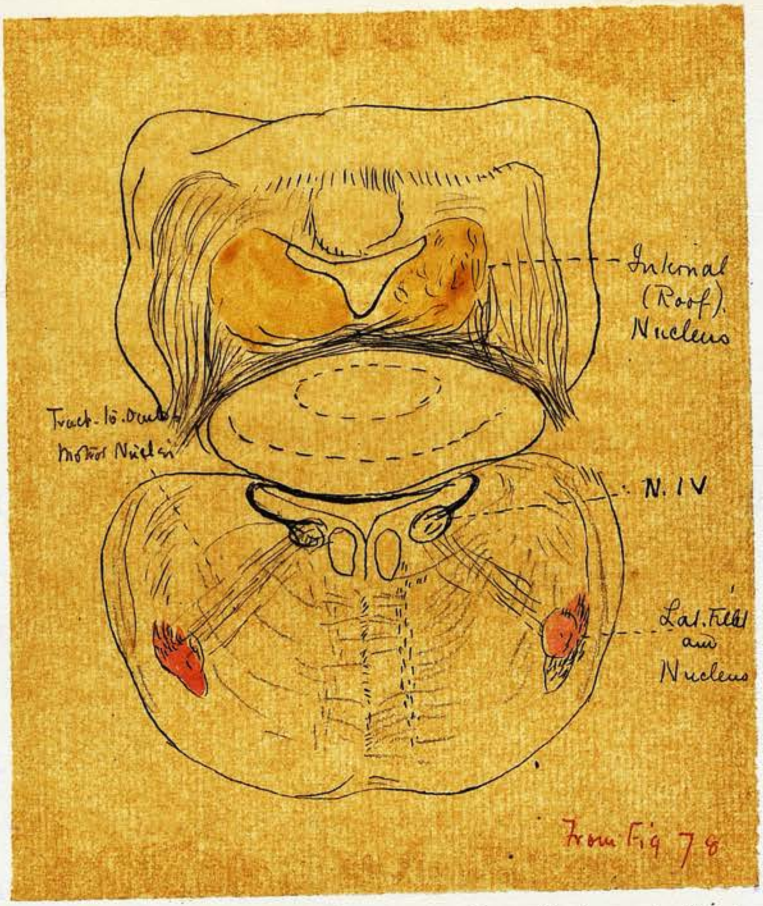
A recent paper by Wallenberg, on the degeneration resulting from an injury to the lateral part of the cerebellum and the cochlear and vestibular nuclei has been of great service in giving definite information concerning the intra-cerebral paths from these nuclei.

The connections of the cochlear nucleus. From its ventro-internal aspect this nucleus gives off throughout its extent a strand of fibres which forms the most dorsal part of the arcuate system and is equivalent to the striae medullares of mammals. (Figs. 72-75) These fibres curve inwards and forwards, parallel to the wall of the ventricle, skirting the small-celled nucleus where present, and taking up a certain number of fibres from it. They then form arcuate fibres and enter the raphe, the most dorsal crossing it at once, while the others bend ventrally in the raphe. The fibres which cross the middle line at once bend backwards on the dorsal part of the opposite formatio reticularis and end in relation to the small-celled nucleus of the opposite side.

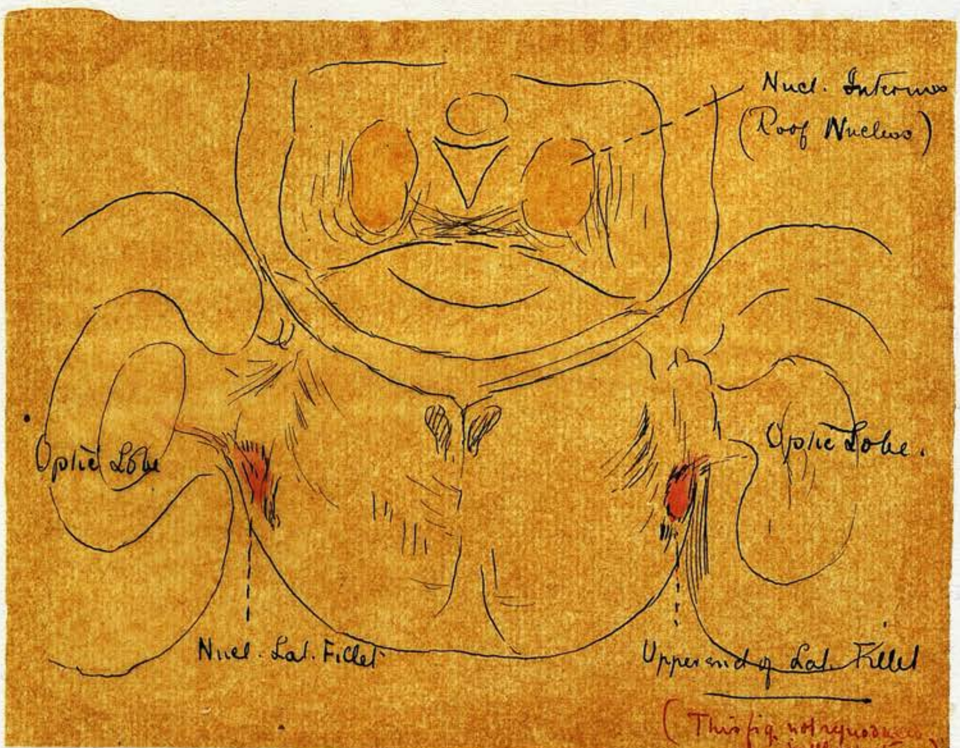
Wallenberg regards them as commissural fibres.

The second group of fibres runs forwards in the raphe towards the ventral part of the medulla. They then bend into the opposite formatio reticularis and pass outwards to end in relation to the cells of the <u>superior olive</u> or to bend upwards to form part of the <u>lateral fillet</u>. Brandis attributed a large number of the cerebellar fibres to this nucleus, but this connection did not appear in the sections examined. The arcuate fibres from the large and small-celled cochlear nuclei seem to follow the same intra-cerebral course. It was not possible to distinguish them from each other by the process employed.

The <u>superior olive</u> is quite a distinct structure in the pigeon. (Fig. 74-75). and, as in the serpent, is continued upwards as the nucleus of the lateral fillet. (In the hen there was a small group of cells in addition to the main olive, on its ventral and inner aspect in the position of the nucleus of the corpus trapezoideum.) It gives off fibres which pass inwards and backwards, towards the grey matter of the floor of the fourth ventricle. These fibres, though they resembled the peduncle of the olive in mammals, were not traced into direct relation to the sixth nucleus, as their course was obscured by the arcuate fibres in the dorsal part of the formatio reticularis.



Transverse section showing lateral fillet tract to oculo-motor nuclei.

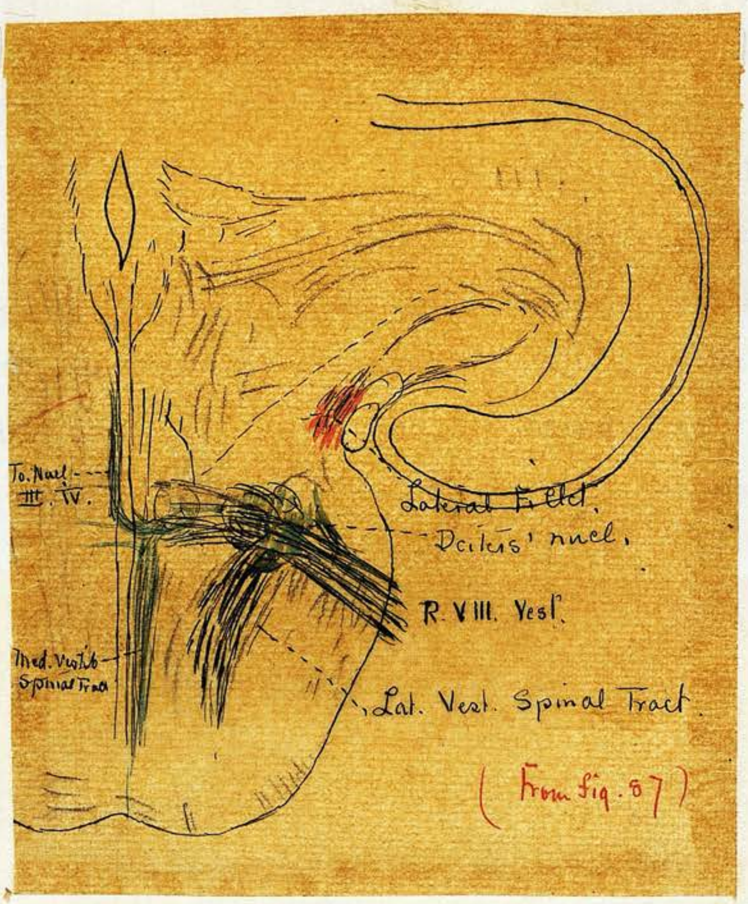


Transverse section showing ending of lateral fillet at base of optic lobe.

The lateral fillet passes obliquely upwards and backwards and is accompanied throughout its course by a nucleus, the lateral fillet nucleus, the direct continuation upwards of the superior olive. Throughout the longitudinal extent of the nucleus fibres, similar to those from the superior olive, are given off on its dorso-internal aspect and pass inwards towards the grey matter in the floor of the ventricle and aqueduct. At the level of the lower part of the oculo-motor nuclei this strand is much more marked, and some at least of its fibres end in relation to these nuclei, others decussate in the raphe and are lost in the opposite formatio reticularis. Bruce has figured this connection and Kölliker also describes it. It is specially well marked in the opossum and rat. (Figs. 98, 122)

The lateral fillet and its nucleus continue to become more dorsally situated until, at the level of the isthmus, the nucleus becomes merged in a nucleus at the lateral portion of the isthmus, but some of the fibres of the fillet are continued upwards to the ganglion laterale mesencephali (fig. 86-88) of the optic lobe, the analogue of the torus semicircularis of the fishes and amphibia. (?)

Some arcuate fibres were seen coursing round the outer side of the inferior root of the fifth



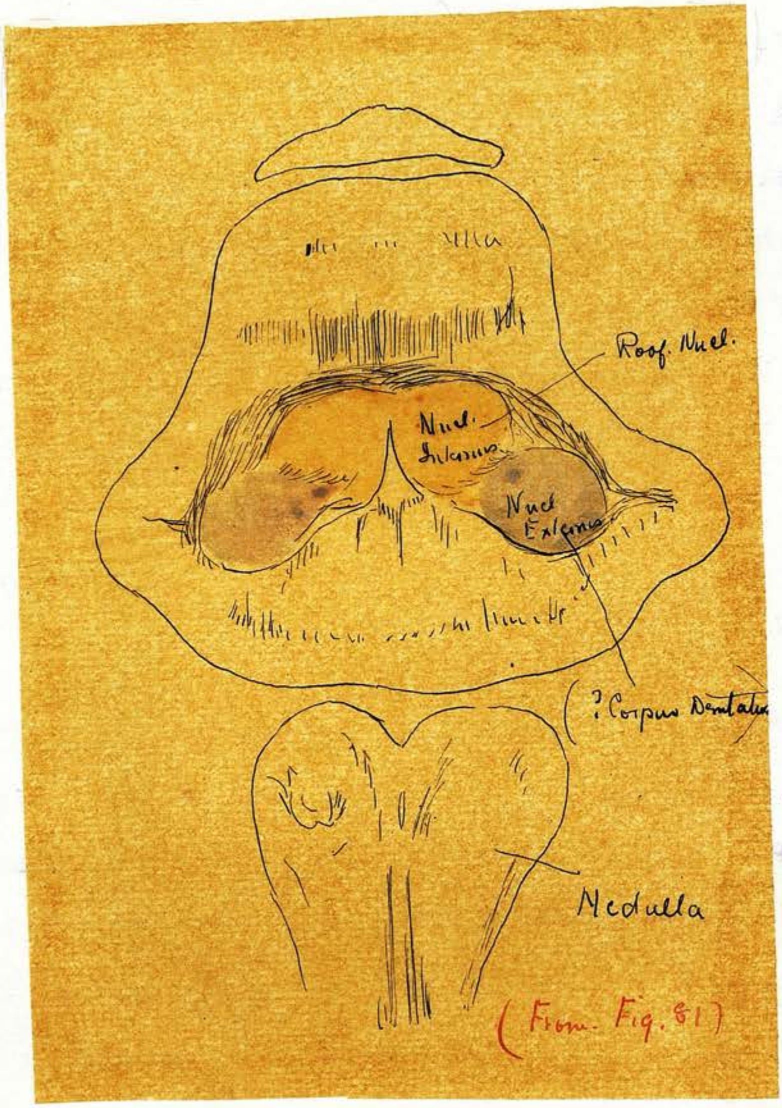
Scheme of connections of vestibular (Deiters') nuclei nerve, but it was impossible to determine whether they rose from the cochlear or the vestibular nucleus. It cannot be said therefore that there was evidence of a corpus trapezoideum in the pigeon, but in the hen, in which the vestibular system is reduced and the cochlear system more prominent, there was a distinct corpus trapezoideum.

The connections of the vestibular nucleus were accurately shown by the degeneration resulting from the destruction of the vestibular nucleus in Wallenberg's case. From the mesial aspect of the nucleus fibres were traced to the posterior longitudinal fasciculus of both sides, and from this tract some fibres were given off to the nucleus of the sixth nerve of the same side. Within the posterior longitudinal fasciculi some of the fibres turned upwards while others turned downwards. Those which turned upwards were in the opposite fasciculus, within which they continued their course as high as the level of the oculo-motor nuclei. They then left the fasciculus and terminated in relation to the nuclei of the fourth and third nerves.

The descending fibres entered the fasciculus of both sides, and forms the median vestibulo-spinal tract. (Figs. 86, 87) Those in the opposite fasciculus terminated in relation to the anterior horn cells in the medulla, while those on the same side passed down into the cord where they endain relation to the cells of the anterior horn at various levels. (Wallenberg.) The lateral vestibulo-spinal tract emerges from the ventral aspect of the group of cells which represent Deiters' nucleus, (Fig. 74) crosses the root of the facial nerve obliquely, and assumes a vertical direction on the posterior aspect of the superior olive. Lower in the medulla it appears as coarse fibres in the antero-lateral column. Wallenberg found this tract degenerated in his case and traced it into the cord.

The cerebellum and its connections.

The avain cerebellum is much more highly developed than that of the amphibians or reptiles, but it does not attain such importance as in the mammals. It is generally regarded as equivalent to the middle lobe of the mammalian cerebellum, but the presence of a lateral nucleus and a superior cerebellar peduncle, indicate that the lateral lobes are represented though they do not form such complicated structures as in the mammals. In the bird the organ is composed of several lobes, divided into smaller lobules by the sulci, and shows the tree-like branching characteristic of the cerebellum. It is peculiar in so far that it contains a ventricle (Fig. 77) which is continuous with the fourth ventricle by a narrow



8a Frontal section showing cerebellar nuclei canal, but widens out within the organ, lying in the middle line and separating the nuclei of the two halves of the cerebellum.

The <u>nuclei of the cerebellum</u> are two in number and were called by Brandis the <u>internal</u> and the <u>external</u> nucleus. (Figs. 81-82 77.). They are large in proportion to the white matter and rounded in form. Unlike the nuclei of the human cerebellum, they are not very distinctly separated from each other, but have the appearance of a single large nucleus, partially divided into two by strands of traversing fibres. Brandis points out that the cells of the two nuclei resemble each other closely. In its lower and most anterior part the external nucleus is not sharply differentiated from the "cerebello-vestibular" nucleus, but is connected with it by means of little irregularly scattered groups of cells, one of which is of larger size than the others and appears as a distinct nucleus called by Brandis the <u>nucleus processus cerebelli</u>. (Figs. 76-77), lying among the tracts to the cerebellum from the medulla and cord. This incomplete separation of the two nuclei was found in two of the lower mammals examined (the mole and the rat). They were more distinctly separated in the cat. The internal nucleus evidently represents the roof nucleus of mammals, but it cannot yet be said definitely that the external nucleus is the analogue of the corpus dentatum.

The connections of the cerebellum may be described as consisting of three groups of fibres.

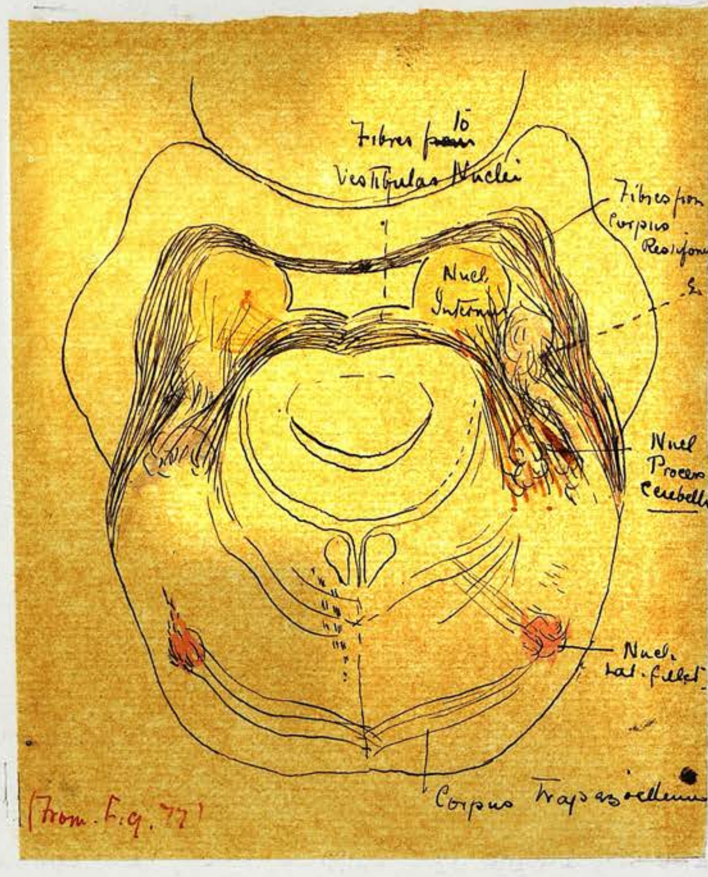
(1) Those connecting the cerebellum with the cord.

(2) Those connecting the cerebellum with the medulla.

(3) Those connecting the cerebellum with the mid and fore-brain.

The connection of the cerebellum with the cord is by means of the restiform body, which contains fibres derived from the cord indirectly by means of the posterior column nuclei and restiform body and from the cord directly by means of the direct cerebellar tract. (Figs.68-78).

These tracts combine to form one strand (which also includes the fibres from the inferior olive to be described below), which passes upwards and obliquely backwards external to the cochlear and vestibular nuclei and enters the cerebellum on its lateral aspect. (Figs.77-79). The fibres then spread out slightly, and the majority pass backwards along the lateral aspect of the external nucleus, giving off fibres as they go to the lateral part of the cortex of the cerebellum. The greater number



Transverse section showing connections of Cerebellum.

of these fibres pass further back to the dorsal part of the cortex, where they terminate, many of them crossing to end in the cortex of the opposite side (Fig. 77.62). A relatively small portion of the fibres of the upper part of the corpus restiform, or <u>inferior peduncle</u>, curve inwards and terminate in the outer part of the external nucleus. (Fig. 77) This is probably the strand from the inferior olive, which is the highest contingent of the restiform body. The fibres of the restiform body are not only distributed to the cortex of the cerebellum at the level at which they enter the organ. They radiate in all directions, curving upwards and downwards within it, so that they are connected with the greater part of the cortex.

The <u>connection with the medulla</u> is also in part by means of the restiform body, inasmuch as the fibres from the opposite inferior olive enter the cerebellum by this path, as has already been mentioned. The most important tract however is that between the cerebello-vestibular nucleus and the nuclei of the cerebellum.

This <u>cerebello-vestibular tract</u> is seen to form internal to the restiform body, at the upper end of the cerebello-vestibular nucleus, a little above the origin of the fifth nerve (Fig. 76). (It will be borne in mind that the ascending fibres are gathered from all parts of the nucleus, and apparently from the nucleus processus cerebelli also. They pass backwards converging as they go into a dense strand which courses round the lateral wall of the fourth ventricle, internal to the external nucleus of the cerebellum. (Figs. 77-78). The lower fibres continue their course almost directly dorsally and terminate in the most dorsal part of the nucleus of the cerebellum, which is at this level only indistinctly divided into two portions. (Fig. 77-78. The higher fibres of this tract end in the internal nucleus of the same side, or decussate ventral to the small cerebellar ventricle and end in the opposite internal nucleus.

This last tract is the equivalent of the cerebello-vestibular tract and is very well marked in the pigeon. It was degenerated in Wallenberg's case doubtless owing to destruction of its fibres as they passed towards the vestibular or cerebello-vestibular nucleus. Wallenberg himself describes the degeneration in his case as rising in the ventral part of the large-celled cochlear nucleus, and Brandis also attributed the greater part of this system to the cochlear nuclei. Unfortunately the former author apparently includes the whole eighth nucleus in the term "cochlear" nucleus, so that it is difficult to know precisely which part is meant, and Brandis recognises no intra-cerebral vestibular nucleus at all. The sections of the pigeon examined proved conclusively that nearly all, if not all, the fibres of the cerebello-vestibular tract are in indirect connection with the eighth, and possibly the fifth nerves through the intermediation of the cerebello-vestibular and vestibular nuclei. Comparison with the analogous tract in other vertebrates indicates that the tract is efferent from the internal nucleus of the cerebellum to the cerebello-vestibular and vestibular nuclei.

The connections of the cerebellum with the mid and fore brain.

No indication of a middle cerebellar peduncle could be seen, but there is a distinct cuperior cerebellar peduncle, formed to a great extent by fibres which radiate from the cortex of the lateral portion of the cerebellum towards the lateral wall of the fourth ventricle. These fibres form a somewhat scattered strand of arcuate fibres, and decussate below the level of the third nucleus. Edinger describes it as decussating at a much higher level and ending in relation to a nucleus, which he calls the red nucleus, in the optic thalamus, but such a course was not found in the sections of the birds examined. The formation of the peduncle from the lateral part of the cerebellum is distinctly seen in birds.

Some external arcuate fibres connecting the upper part of the cerebellum with some small groups of cells in the ventral part of the upper medulla probably represent the <u>middle-cerebellar</u> peduncle. They were not easily distinguished from the fine fibres which bend dorsally out of the ventral columns of the cord at this level to enter the valvula cerebelli. These latter fibres were present also in the lower vertebrates already examined and have already been fully described. As they form only an indirect connection if any with the cerebellum there is no necessity to give a detailed account of them.

Brandis, who examined many orders of birds found that there was little variation in the relations of the eighth nerve system. The only difference was in the relative development of the cochlear and vestibular roots and nuclei. The vestibular system is best developed in the rapidly flying and poising birds. The cochlear system is most complicated in the domestic birds.

The Eighth Nerve in Mammals.

Plates. XXIX- XLIV

Before entering on the description of the eighth nerve and its connections in mammals it must be stated that this portion of the subject has been so fully investigated and described by others that the work was mainly one of reference, in many respects. This is specially true of the human medulla which has therefore only been figured in so far as it illustrates this special work, while the medullae of the lower mammals, which are less well-known, have been more fully illustrated since they show the transitional stages in the development of the various structures.

The number of investigators in this field is so great, and their work so well known, that it has been at once impossible and unnecessary in the limited scope of this thesis to give all the references which arise in the study of the subject. I have therefore refrained from doing so except in regard to the most recent work. It has also been impossible to deal with the subject of the mammalian medulla in any great detail, and I have therefore limited myself to the simplest description which was compatible with the nature of this thesis.

The eighth nerve in Mammals.

The eighth nerve and its connections attains its fullest development in mammals, forming the most extensive system of the medulla. It varies considerably in the different species, according to the development of the functions of hearing and equilibration, and for this reason several types were selected for illustration. These included the opossum, the mole, the calf, the rat, the cat and the human foetus, - these forms being selected as fairly representative of the mammalian series. The most obvious differences in the eighth nerve system of mammals as compared with that of the lower vertebrates are:-

(1) The marked lateral and ventral situation of its nuclei.

(2) The relative increase in size of the restiform body, and its interpolation between the cochlear and the vestibular nuclei in some species.

(4) The change in the character of the vestibular root, which becomes a single compact strand.

(5) The large size and complexity of the cerebellum, the greater individualisation of its nuclei and increase in importance

of its peduncles.

(6) The increase in importance of the inferior olive and the arcuate system connecting it with the cerebellum.

It is obvious, when the medullae of the lower and higher vertebrates are compared, that the first five of these changes are inter-dependent,— that the changes in position necessarily result from the modifications in size which the parts undergo. Thus the enlarging cochlear nucleus is prevented from growing backwards by the growth of the lateral lobe of the cerebellum. The only direction in which it can increase is outwards and ventrally, but here it is met by the restiform body, which is making its way by the shortest path from the cord to the cerebellum. The cochlear nucleus is thus forced to extend outside the corpus restiforme, and therefore passes round this structure and forms on its outer and ventral surface. Reference to the figures of the medulla of the opossum and the rat (~~figs.~~ Plates XXIX & XXXIV) will explain this.

The condensation of the vestibular root is due to the fact that the ventral growth of the cochlear nucleus and the enlargement of the substantia gelatinosa and fibres of the inferior root of the fifth nerve, form two out-growths on the lateral and ventral aspect of the medulla, which leave between them a narrow space between which the vestibular root must travel in order to arrive at its nucleus. This condition is present in most mammals, being best marked in the varieties in which the fifth and the eighth nerve systems are best developed (see the figures of cat, rat and human foetus) Plates XXXIX. XXXIV. XLII. XLIII. and less evident in the forms in which the inferior root of the fifth nerve and the cochlear nuclei are relatively less developed. (see figures of the opossum and the calf Plates. XXIX. XL.).

By this re-arrangement of parts, the cochlear nuclei are divided from the remainder of the medulla by the entering vestibular nerve and the restiform body, and present the isolated appearance characteristic of the mammalian medulla.

The eighth nerve of the mammals is divided into a <u>cochlear and a vestibular</u> root. The cochlear root develops later than the vestibular root and enters the anterior acustic nucleus, (Figs. 89-96 123-129. etc.) some of its fibres passing on to enter the tuberculum acusticum (Figs. 93. 94) The fibres divide immediately on entering the nuclei into ascending and descending branches. Some of the descending branches end in the tuberculum acusticum, but the greater number end in relation to the cells of the anterior acustic nucleus. The descending branches end also mainly in relation to the cells of the anterior acustic nucleus. Both branches are short and give off a few collaterals.

The vestibular root medullates earlier than the cochlear root. It enters the medulla close to the latter, and internal to it. Its lowest fibres appear at a higher level than do the most inferior cochlear fibres, and its highest limit is about the level of the facial nerve. Its size varies in different species. In the mole, for instance, it is relatively small. (Figs. 103-106).

It terminates in relation to several nuclei:-

(a) Deiters' nucleus.

(b) The cells among the fibres of the inferior root, the inferior vestibular nucleus.

(c) Bechterew's nucleus.

(d) The funiculus cuneatus.

(e) The dorsal nucleus of the eighth nerve.

To reach these nuclei the nerve passes in between the inferior root of the fifth nerve and the restiform body in the manner described above. At the dorsal boundary of the inferior root of the fifth nerve, its fibres spread out in a fan-shaped manner, (Figs. 117-127, 133-138), and divide into ascending and descending branches.

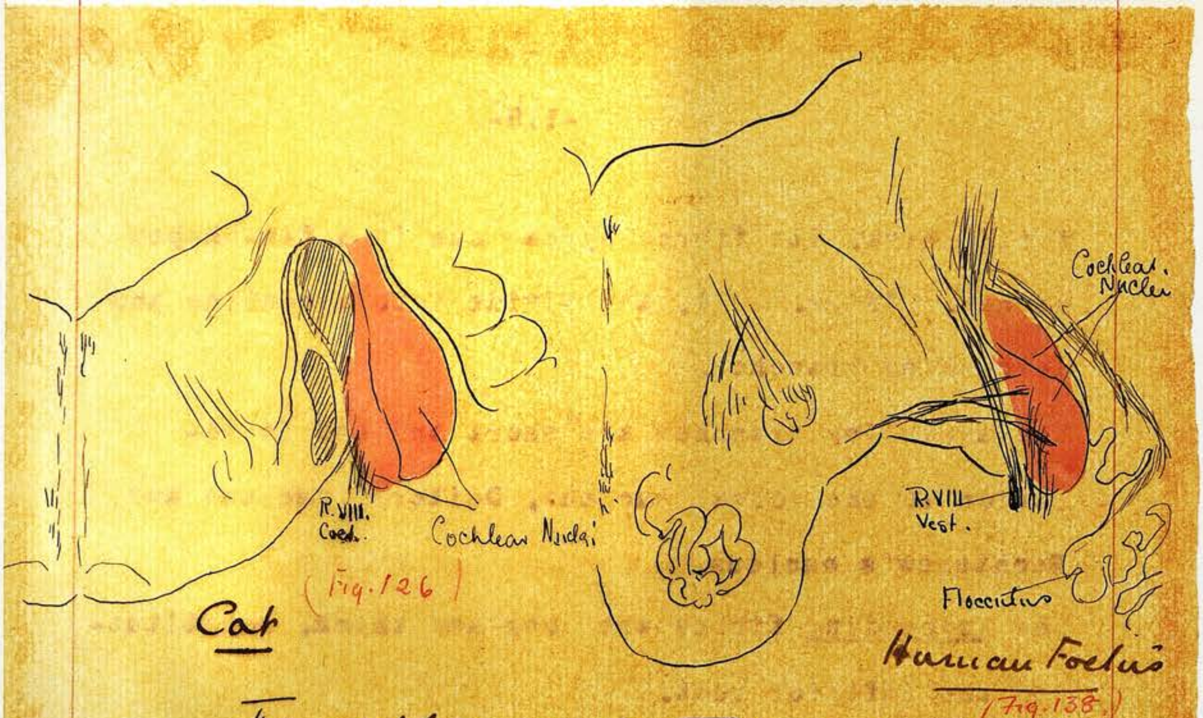
The ascending branches are short and end in relation to the dorsal nucleus, Deiters' nucleus and Bechterew's nucleus.

The <u>descending</u> fibres are long and thick, constituting the inferior root.

The <u>inferior</u> root of the eighth nerve in mammals forms a well marked area internal to the restiform body, dorsal and internal to the inferior root of the fifth nerve. It is composed of fibres which turn in a longitudinal direction arranged in loose bundles with a wavy course. (fig. 100). These on transverse sections appear as little groups of cross-cut fibres. The root becomes smaller as it descends, giving off both collaterals and terminal branches to the cells placed among its fibres. Its lowest fibres end in close relation to the nucleus cuneatis.

The <u>nuclei of the eighth nerve</u> in mammals form two important groups, the <u>cochlear nuclei</u> and the <u>vestibular nuclei</u>.

The <u>cochlear nuclei</u> reach their highest perfection in certain mammals, (the rat, cat, rabbit etc.).

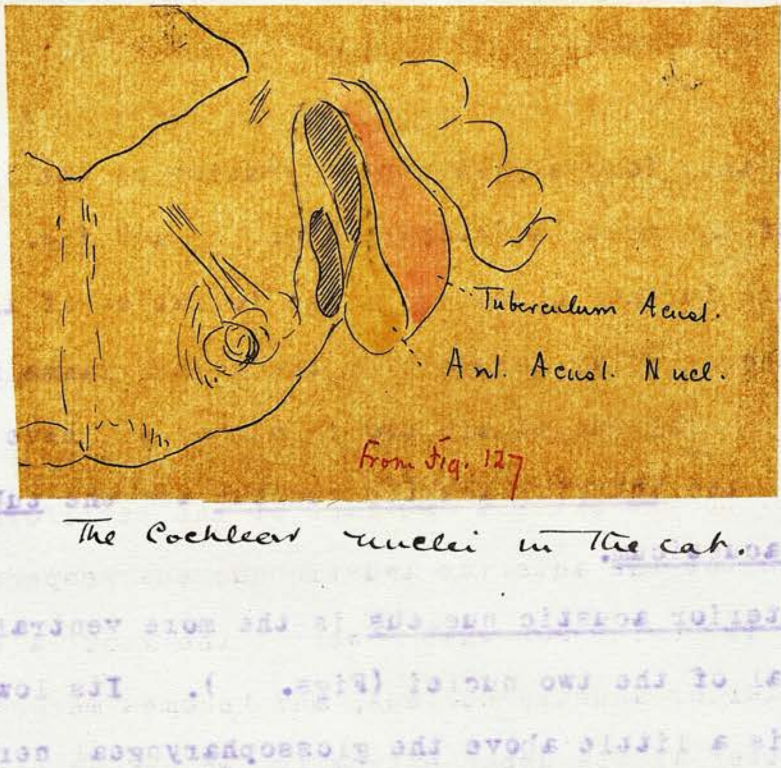


The cochlear nuclei in the cat and man.

They are placed as already said on the lateral aspect of the medulla, immediately external to the restiform body and the entering vestibular nerves and are in close relation with the most ventral lobe of the cerebellum. In man, in whom this lobe of the cerebellum is very highly developed and the cochlear nuclei small, the latter are entirely hidden from view when the parts are in position, but in certain lower mammals, where the nuclei are large and the lateral lobes of the cerebellum are relatively small, they form a prominent elevation on the lateral part of the medulla (compare fig. 127 and fig. 138).
They are further obscured by the formation of the middle cerebellar peduncle in the higher mammals.

The nuclei are two in number and have been called the anterior acustic nucleus and the tuberculum acusticum.

The anterior acustic nucleus is the more ventral and internal of the two nuclei (Figs. ~~132~~ 127). Its lowest level is a little above the glossopharyngeal nerve, being somewhat higher than the inferior extremity of the tuberculum acusticum. Its upper limit varies somewhat in different mammals, but as a rule it extends upwards, gradually increasing in size, for some distance, and then again diminishing, until the level of the emerging root of the facial nerve, where it ceases



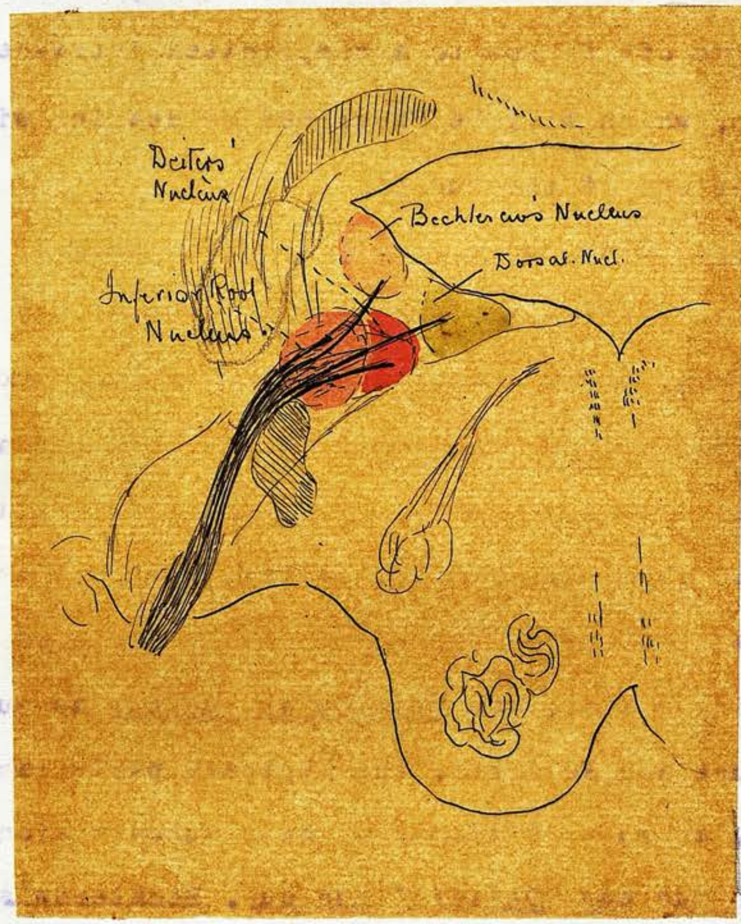
The Cochlear nuclei in the cat.

to appear. In its lower portion it is distinct from the tuberculum acusticum, but in its upper part it gradually merges in the latter so that the two are indistinguishable. The nucleus is oval in shape with a rounded ventral extremity projecting on the surface of the medulla and a more tapering dorsal extremity which inserts itself between the inferior root of the fifth internally and the tuberculum acusticum externally. In man the growth of the cerebellum and the development of the transverse fibres of the pons combine to render the nucleus more deeply placed and less visible on the surface of the medulla than it is in lower forms.

The tuberculum acusticum, is also an elongated nucleus lying obliquely on the lateral aspect of the medulla applied to the external surface of the restiform body and of the anterior acustic nucleus respectively. It begins somewhat lower in the medulla than the anterior acustic nucleus, and becomes merged in the latter at its upper extremity, which, as said, is near the level of the emerging root of the facial nerve. Its free extremity does not extend so far ventrally as does the anterior acustic nucleus, and dorsally it merges insensibly into the strand of fibres which curves round the restiform body at this level. Its lateral aspect is in close relation to the most ventral lobe of the cerbellum, the floc-culus, (Figs. 96. 106. 138) where that exists, and receives some fibres from the latter structure. These two nuclei form the terminus for the fibres from the cochlear nerve, the anterior acustic nucleus receiving the majority, and give off fibres to a complicated intra-cerebral system, which will be described in dealing with the connections of the nuclei.

The vestibular nuclei are placed dorsally in the medulla, internal to the cochlear nuclei and resti-form body, dorso-internal to the inferior root of the fifth nerve. These nuclei are regarded as divided into four parts. These are not distinctly divided from each other, however, but form an ir-regular body of cells, and might be included under the single term, the vestibular nucleus as suggested by Bruce and Kölliker, the separate parts ranking merely as sub-divisions. These sub-divisions are:- dorsal nucleus, Deiters' nucleus, Bechterew's nucleus, and the nucleus of the inferior root. (See figs. of Transverse. Cal. Rat. Calf, Human Foetus for Vestibular Nucleus.)

The dorsal nucleus, has received a number of synonyms which need not be mentioned here. It forms the internal and more cellular part of the common vesti-bular nucleus, and receives some of the fibres of the vestibular nerve (figs.). It lies immediately ventral to the floor of the fourth ventricle, external



Scheme of nuclei of vestibular nerve.

to the dorsal vagus nucleus, in the lower part of its course, and internal to the inferior root of the eighth nerve throughout its extent.

Deiters nucleus' is a group of cells, not arranged in a circumscribed nucleus, but scattered amongst, and ventral to, the fibres of the inferior root in its upper portion. The cells of this nucleus are easily recognised by their large size, and in Golgi sections by the thickness and length of their dendrites.

Bechterew's nucleus, as it is called in man, corresponds to the cerebello-vestibular nucleus of lower forms. It is placed dorsal to Deiters' nucleus, in the lateral wall of the fourth ventricle. It consists of cells, smaller than, but otherwise similar to those of Deiters' nucleus. In man the cerebello-vestibular nucleus is reduced to a small group of these cells and forms an upward prolongation of Deiters' nucleus, but in some of the lower mammals forms a large group of scattered cells traversed by many horizontal fibres on their way to or from the cerebellum. It is known in the fishes as the Uebergangsganglion. This nucleus receives mainly the ascending divisions of the fibres of the vestibular nerve.

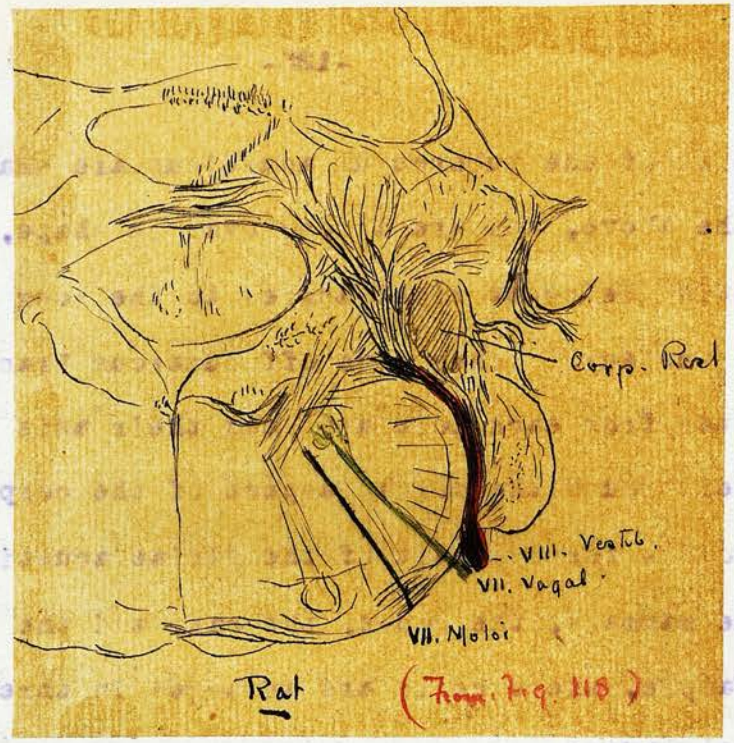
The nucleus of the inferior root is represented by numerous cells which lie scattered among the fibres of the inferior root of the eighth nerve, and are in relation with the end-tufts of the collaterals and terminal branches of this root.

The cells of the eighth nucleus in mammals have been most minutely described by Kölliker, Cajal and Held, and it is beyond the province of this thesis to enter upon a full description here. All that will be done therefore is to give briefly the more important points bearing on the subject under discussion. The cells of the anterior acustic nucleus are large and rounded or oval. In the anterior part of the nucleus their dendrites are few, but in the posterior part the cells have many large branching dendrites, most of which emerge on one side and pass in one direction, viz:- inwards. The axis cylinders of these cells all eventually enter the corpus trapezoideum, the majority passing ventrally, but some passing dorsally round the restiform body in a manner to be afterwards described. Held and Cajal state that the entering fibres of the vestibular root sometimes form "baskets" round these cells, resembling the "fibre-baskets" round Purkinje's cells in the cerebellum.

The cells of the tuberculum acusticum are smaller than the above, and are a long oval in shape, their long axis being at right angles to the long axis of the nucleus. They give off numerous branching dendrites from each pole and send their axis cylinders round the dorsal aspect of the corpus trapezoideum forming part of the striae acusticae. In some mammals, the mouse, the cat, and the rat for example, these cells are arranged in three parallel layers.

The cells of <u>Deiters' nucleus</u> are remarkable for their great size and for the length and thickness of their dendrites. They closely resemble the large motor-cells of the anterior horn of the cord. The cells of the vestibulo-spinal nucleus and of the inferior root are mainly of medium size and multipolar, they present no special characteristics.

The <u>motor facial nerve</u> of the mammal is too well known to require description here, but its accompanying sensory portion, the pars intermedia Wrisbergii (figs. 126, 118, 138), may be mentioned briefly. This nerve is now generally regarded as ending in an upward continuation of the cells of the nucleus of the fasciculus solitarius, the latter strand being now accepted as the homologue of the fasciculus communis in the frog, and of the lobus vagi in the fishes.



Transverse section showing relation of the motor and vagal (pars intermedia) root of the VIIth nerve to the vestibular root of the VIIIth nerve

The pars intermedia is, therefore, as has been already stated, the analogue of the vagal root of the facial in the lower vertebrates. In mammals it enters the medulla in close relation to both seventh and eighth nerve, being inserted between the motor seventh root and the vestibular root of the eighth nerve (Figs.116), which is, it will be remembered, the same position it occupied in the fishes and the frog. It undoubtedly is present in the interven-ing orders between amphibians and mammals although not figured here. In some of the mammals this nerve is not in such close relation to the vesti-bular root as in others. The difference is due to the greater development in some species of the inferior root of the fifth nerve, which divides the pars intermedia from the eighth nerve, and also to the fact that in most mammals the vestibular root passes entirely dorsal to the inferior root of the fifth nerve, instead of partially piercing it. These two factors combine to separate the two roots. The nucleus of the pars intermedia lies in the dorsal part of the formatio reticularis on the external aspect of the motor root of the facial nerve.

The connections of the eighth nerve in mammals.

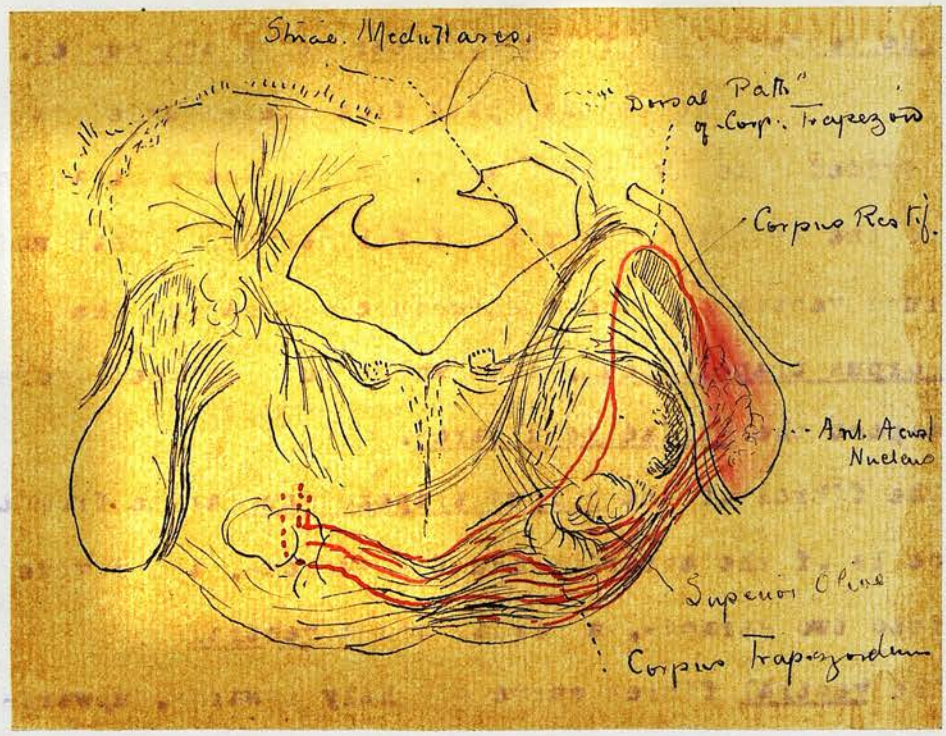
The principal difference between the birds and mammals as regards these connections, is the great increase in the corpus trapezoideum and its associated nuclei, and, in man the addition of a special strand of fibres, the striae acusticae.

The connections of the cochlear nerve and nuclei.

The central path from these nuclei is divided into two parts according to their relations to the restiform body and fifth nerves. That which runs ventral to these structures is called the corpus trapezoideum, that which runs on their dorsal aspect the striae medullares.

The fibres of the corpus trapezoideum arise from the cells of the anterior acustic nucleus, and divide into two strands, a dorsal and a ventral.

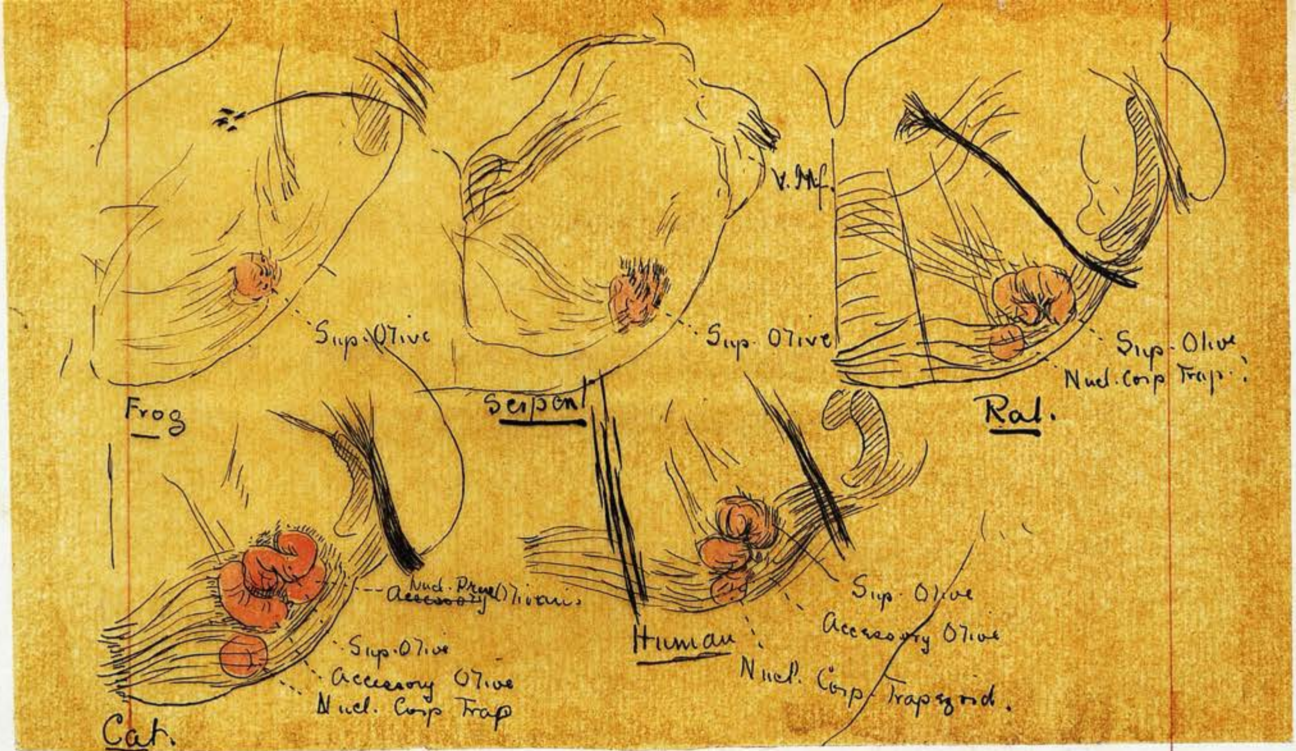
The ventral fibres curve slightly inwards, upwards and ventrally, being in immediate relation in the first part of their course to the inferior root of the fifth nerve. Some of the fibres then enter the superior olive or its accompanying nuclei (the accessory olive and the nucleus of the corpus trapezoideum) of the same side, many fibres, according to Held, being continued upwards without interruption into the lateral fillet. The majority of the fibres cross the raphe and partly terminate in the superior olive and the associated nuclei of this side, partly pass upwards into the lateral fillet. There is as yet considerable doubt as to whether any



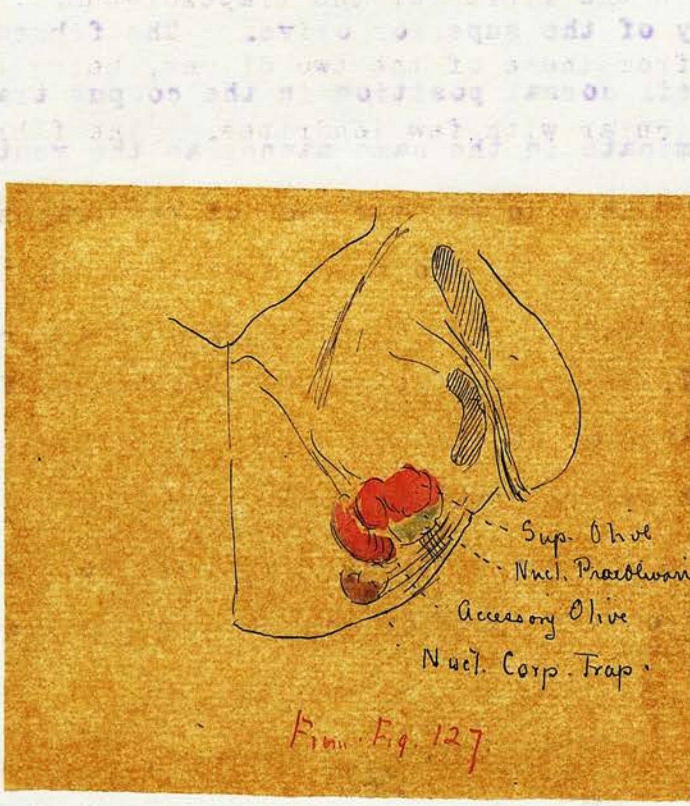
Scheme of connections of cochlear nucleii by the Corpus Trapezoideum

of the fibres of the corpus trapezoideum extend to the opposite anterior acustic nucleus. This structure, the corpus trapezoideum, reaches its highest development as far as is known in the cat, (figs.127.128. where it forms a broad band of fibres stretching from side to side of the medulla.
The dorsal fibres of the corpus trapezoideum (Figs.95. 105. 116 126 132) arise from the cells in the posterior part of the antero acustic nucleus and curve backwards along the dorsal aspect of the corpus restiforme. They then curve sharply ventrally again, either piercing the restiform body or passing completely round it, and traverse the substantia gelatinosa of the fifth nerve in boldly curving strands to join the ventral portion of the corpus trapezoideum in the near vicinity of the superior olive. The fibres maintain their dorsal position in the corpus trapezoideum and terminate in the same manner as the ventral fibres. This dorsal division of the trapezoid body is called by Held, who first described it, the "dorsal path". It is very marked in the cat, rat and calf, and less distinctly in the human foetus. An explanation of its nature, fully establishing Held's views is given on page (155).

The nuclei which lie in the course of these fibres from the anterior acustic nucleus are 3 in number, the



Showing development of the superior olive.



Showing Superior Olive and accessory nuclei in the cat.

superior olive, the accessory olive and the nucleus of the corpus trapezoideum.

The superior olive, varies in size and shape in different mammals. In the opossum it is merely a rounded nucleus, (fig. 95) in the rat it has a faint appearance of convolution (Fig. 117), and in the cat and rabbit it is large and distinctly convoluted. In the calf (Fig 134) and in man (Fig 139) it is much simplified.

The accessory olive when present is placed on the inner, ventral aspect of the main olive, of which it appears to form a subdivision, its structure being similar to that of the olive.

The nucleus of the corpus trapezoideum lies ventral and internal to the other two nuclei, deeply imbedded in the fibres of the corpus trapezoideum. Its cells differ from those of the two olives, being large and vesicular with few dendrites. The fibres which terminate in relation to these cells, end in peculiar plates or cups, into which the body of the cells are fitted, and according to Cajal are derived from the cells of the anterior acustic nucleus. The nucleus is present in man, but the peculiar cells and cupped fibres have not been found as yet.

Cajal and Kölliker have also described a small pre-olivary nucleus in immediate relationship to the main olive on its ventral aspect.

Scheme of Striae medullares, including the "dorsal path" of Held, from anterior acoustic nucleus.

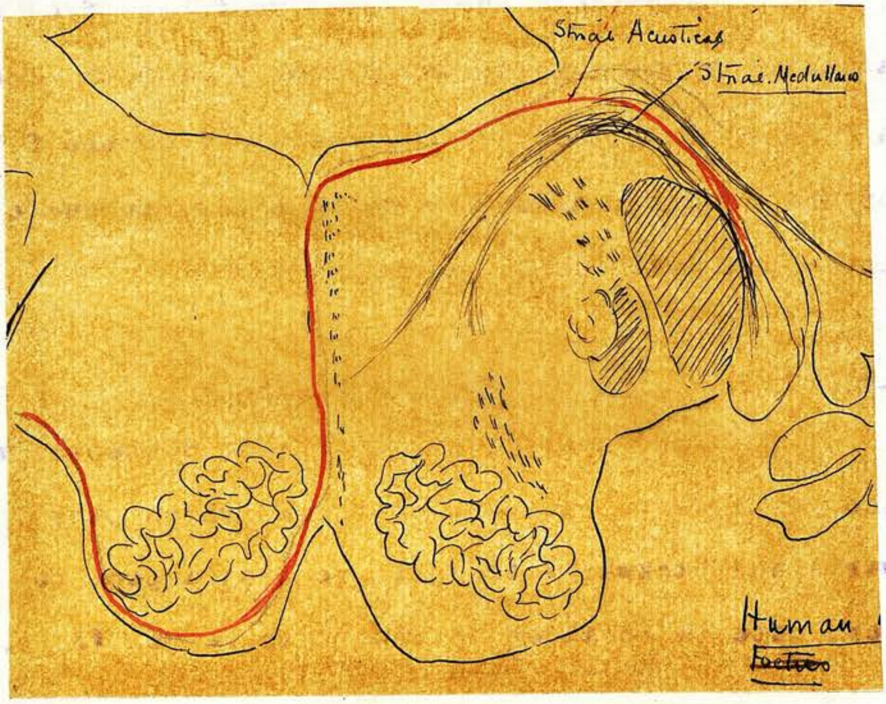
All these nuclei receive fibres from the anterior accessory nucleus probably of both sides, and in addition receive collaterals from the fibres of the corpus trapezoides, which enter the nuclei on their ventral aspect. (fig. 134).

<u>The peduncle of the superior olive.</u>

The superior olive is also connected with the sixth nerve by means of fibres which pass inwards and backwards from its ventral aspect to terminate in relation to the sixth nerve. (Figs. 119.127)

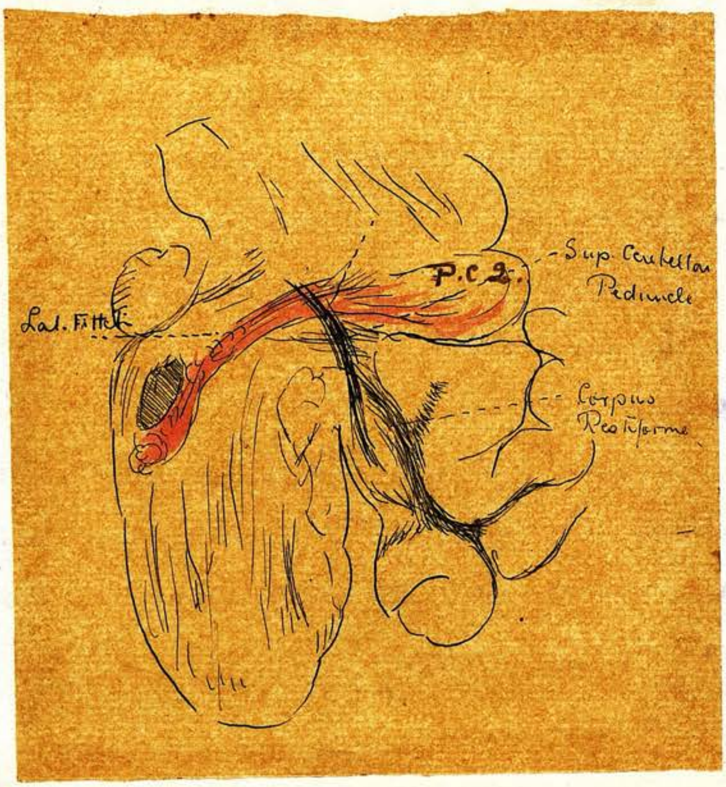
<u>The striae medullares</u>, are the fibres from the tuberculum acusticum which curve round the restiform body in close relation to the dorsal part of the corpus trapezoideum, from which they are distinguished by their finer calibre (Fig. 116, 132). After curving round the restiform body they pass inwards and forwards, to end partly in relation to the superior olive of the same side, (Fig. 96, 6) partly in relation to that of the opposite side, (Fig.) after crossing the raphe. It is doubtful whether these fibres turn upwards in the lateral fillet or end in the superior olive.

Some of the striae medullares according to Kölliker bend upwards in the opposite tegment and pass upwards as a tegmental tract. Their termination is unknown.



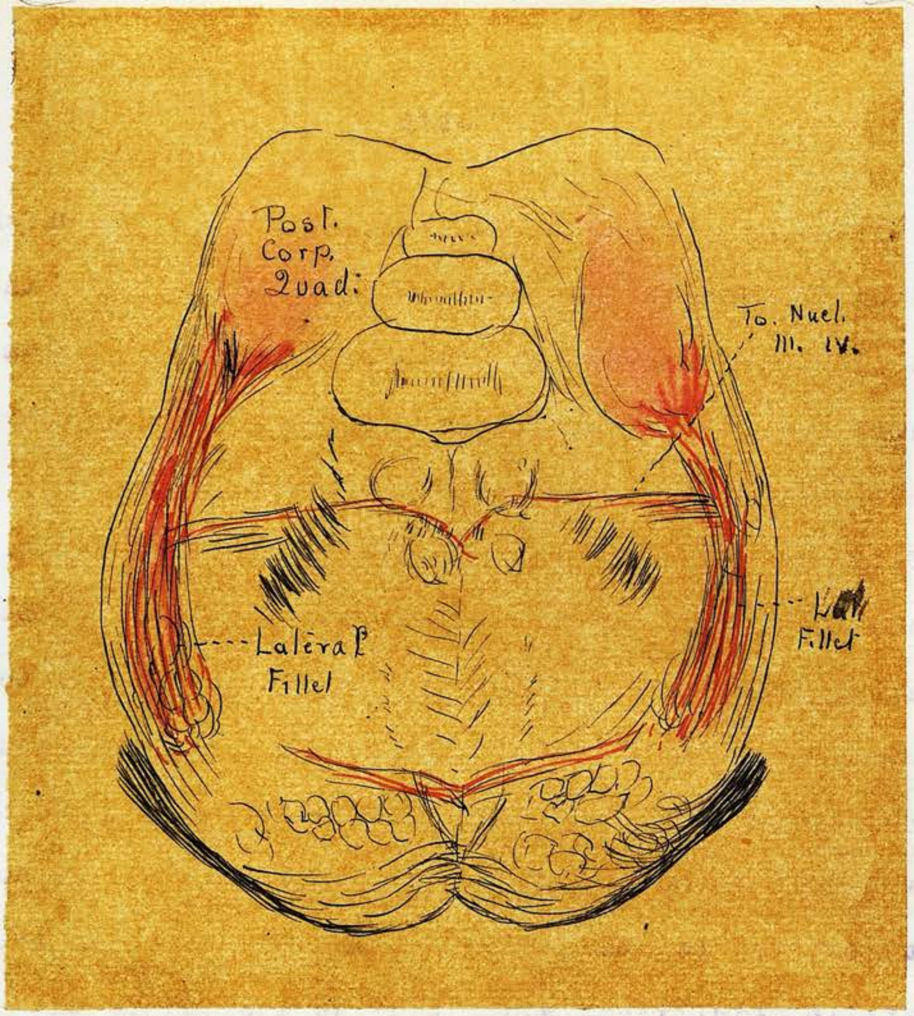
Scheme of Striae Acusticae in Man.

Sagittal section (mole) showing the lateral fillet



Kölliker has further described a tract in man which rises in the tuberculum acusticum, curves round the restiform body, and runs forwards and inwards under the floor of the fourth ventricle. Here the fibres enter into relation with the nucleus teres, and afterwards pass into the dorsal part of the raphe. They run ventrally through the whole extent of the raphe, curve round the periphery of the medulla to enter the restiform body of the opposite side, and presumably to enter the cerebellum with it. Kölliker calls these the <u>striae acusticae</u>, a term which should be reserved for this tract. The more general term "striae medullares," would thus be applied to the dorsal connections of the cochlear nucleus in lower mammals, and in man, to those, other than the striae acusticae. It is interesting to note that Kölliker states that these auditory fibres (the striae acusticae in man) are connected with the nucleus teres which is evidently the analogue of a nucleus placed in the lateral wall of the fourth ventricle in birds, (fig 75) this being itself simply a sub-division of the large celled cochlear nucleus.

The <u>lateral fillet</u> in mammals (Figs. 100-109) does not differ greatly from that of lower vertebrates. It is accompanied in all cases by the lateral fillet nucleus, the direct upward continuation of the



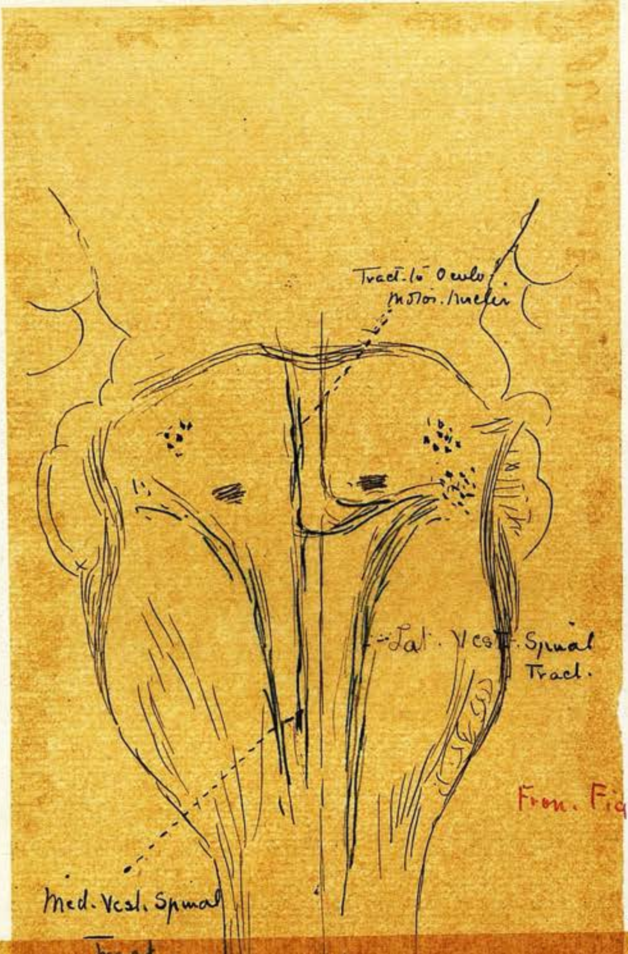
Transverse section of (rat.) showing lateral fillet, tract to oculo-motor nuclei and the Posterior corpus quadrigeminum superior olive, and is a relatively larger structure in mammals than in the lower vertebrates. As in the bird fibres are given off from its nucleus towards the grey matter of the ventricle. (Figs.78) These are specially numerous at the level of the oculo-motor nuclei where they form a distinct strand. (fig. 122). The fillet ends in the posterior Corpus Quadrigeminum (Figs 100.109.98.+122.)

The connections of the vestibular root in mammals resemble those already described in the lower vertebrates and fully maintain their importance in a comparison with other parts.

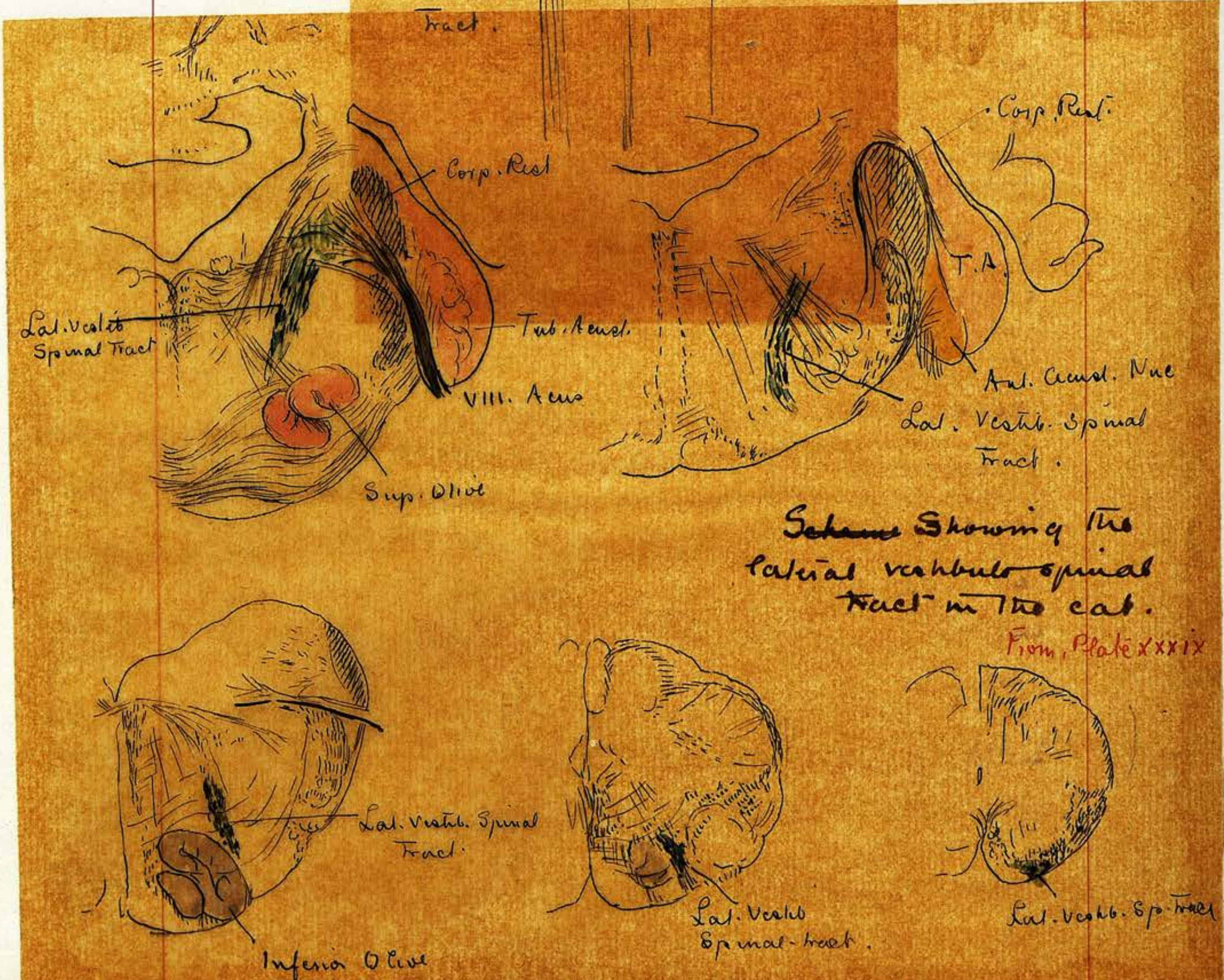
The main connection is that of Deiters' nucleus, which as in other forms gives off fibres to the posterior longitudinal fasciculus of both sides, and to the antero-lateral column of the medulla and cord of the same side. The course of these fibres has been amply proved and fully described by Bruce, Held, Ferrier and Turner, Risien Russel, Thomas, Boyce and Marchi, so that only a brief outline need be given here.

The fibres from Deiters' nucleus to the posterior longitudinal fasciculus. These pass inwards from the nucleus towards the raphe as arcuate fibres, giving off by the way a small strand to the Sixth nucleus. The fibres then enter the posterior

Scheme (Rat) showin
Connections of Vestib
nuclei with cord an
oculo-motor nucle



From. Fig. 123.



~~Scheme~~ Showing the lateral vestibulo spinal tract in the cat.

From. Plate XXXIX

longitudinal fasciculus of the same and of the opposite side, and bend either upwards or downwards, the majority taking the latter course. Those which bend upwards are mainly in the opposite fasciculus, and end in relation to the opposite oculo-motor nuclei. Those which pass downwards are mainly in the fasciculus of the same side and are continued into the cord, ending in relation to the large motor cells of the anterior horn, as low as the lumber segments. The fibres which pass downwards in the opposite fasciculus cannot be traced so far, but have been seen in the dorsal segments of the cord. These descending fibres from Deiters' nucleus are now known as the median vestibulo-spinal tract. The ascending tract to the oculo-motor nuclei has not yet received a name.

The lateral vestibulo-spinal tract presents the same appearance as in other vertebrates. It arises from the cells of Deiters' nucleus, curves forward towards the dorsal aspect of the superior olive, crossing part of the motor root of the facial nerve Plates. XXXIX. XL. etc (~~Figs.~~), as it does so. It passes internal to the superior olive (Figs.128-134) and bends into a longitudinal direction. At lower levels it occupies a position on the dorso-lateral aspect of

Showing the development of the cerebellar nuclei.

the inferior olive, and still lower, appears in the antero-lateral column of the cord. (Figs. 123 – 129) The tract is well seen in the figures of the rat, the cat, the calf and the human foetus. (Plates 39-40-41-42.) (~~Figs.~~).

The connections of the cerebellum.

The cerebellum in mammals attains a large size, relatively to the medulla. Its appearance is well-known and needs no description here. It differs from the cerebellum of lower forms in the increase in the number of its nuclei and in their greater individualisation. In the lower mammals there are evidently two large nuclei, but these are indistinctly separated from each other, and in some cases are almost continuous with the nuclei of the eighth nerve, (Figs. 95.116). In higher forms the lateral nucleus assumes a more convoluted appearance, and the internal nucleus becomes more condensed and distinct. In man the lateral nucleus has formed numerous convalutions and closely resembles the inferior olive in appearance, while the internal nucleus is relatively much smaller and is situated above and internal to the former. The internal nucleus in man is known as the roof nucleus (Fig. 140) and the external as the corpus dentatum (Fig. 140.142). Between the two are two smaller nuclei, the nucleus globosus and emboliformis, of which an indication is seen in the calf. (Fig. 134).

The connection of the cerebellum with the other parts of the nervous system is made by means of its peduncles, of which, in mammals, there are three, inferior, middle and superior. Through these peduncles the cerebellum enters into communication chiefly with:-

(a) the cord directly, by the ventral and lateral cerebellar tracts.

The Cord.

(b) the cord indirectly, through the posterior column nuclei and the arcuate system.

"

(c) the inferior olive, by means of the olivary arcuate system.

The medulla.

(d) Deiters' and Bechterew's nuclei

"

Pons. (e) The nuclei of the pons, by means of the middle cerebellar peduncle.

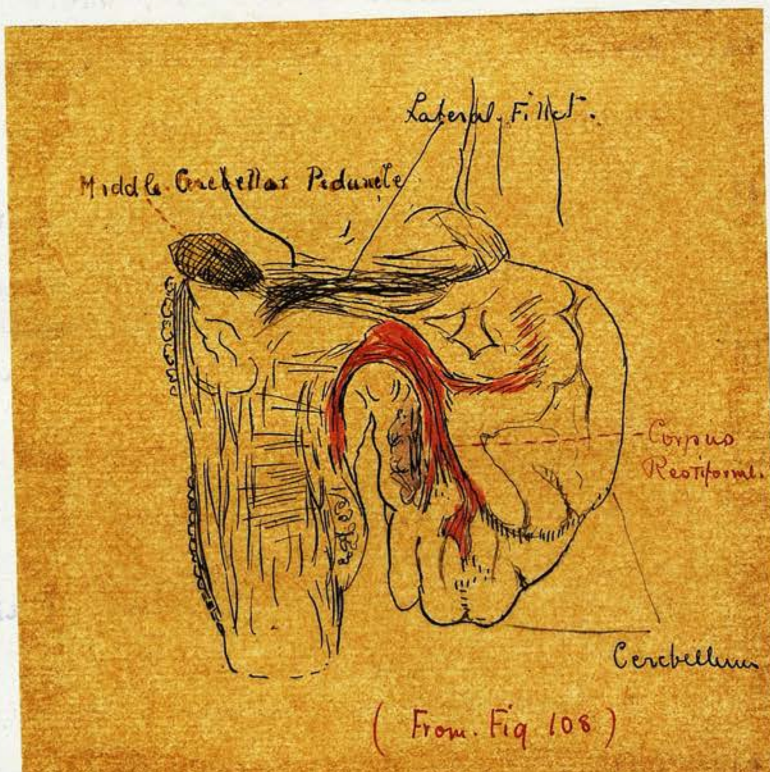
"

Mid-brain.

(f) The red nucleus and possibly the external nucleus of the optic thalamus.

"

The composition of the restiform body as it occurs in mammals is now known, and has been fully described by Kölliker, Bruce, Obersteiner and others. It contains fibres from the posterior



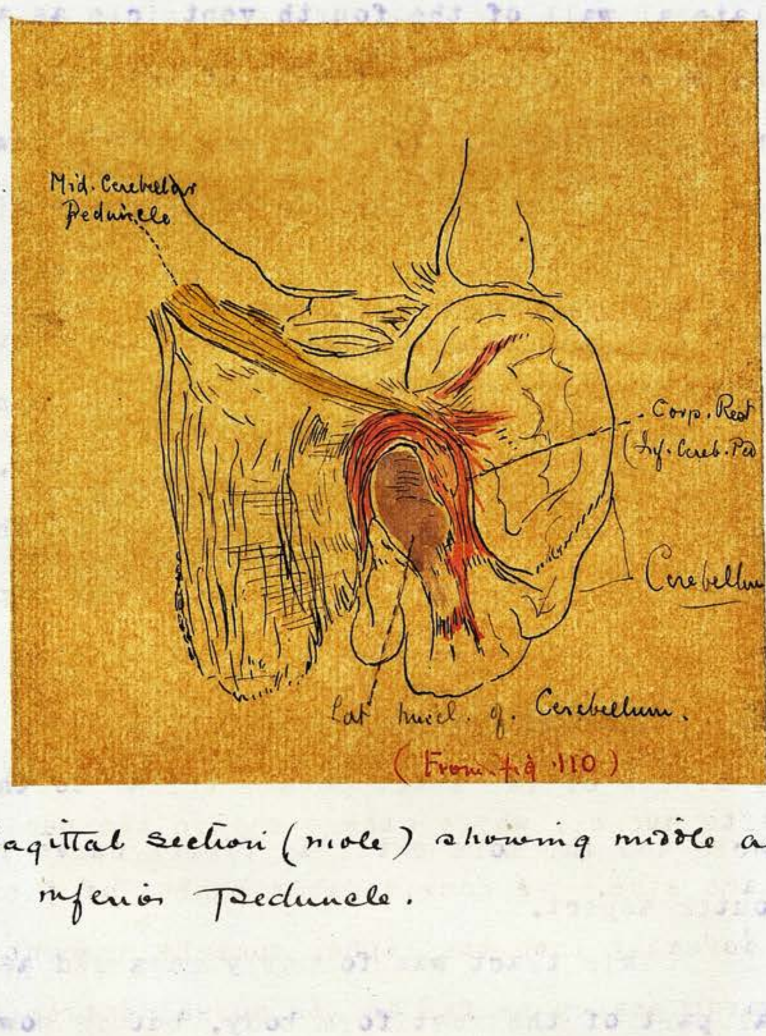
Sagittal section (mole) showing restiform body. (inferior peduncle).

column nuclei of both sides, from the dorsal cerebellar tract, the nucleus lateralis and the inferior olive. These fibres are all collected into a compact strand which passes upwards on the lateral aspect of the medulla (in man the dorso-lateral aspect), inserts itself between the vestibular and the cochlear nuclei and terminates by curving upwards and backwards to the cerebellum, where its fibres radiate in all directions. (Figs. 108.99) As will be seen from the figures it enters the medulla at a higher level than the superior cerebellar peduncle, but somewhat lower than the middle peduncle. Within the cerebellum its fibres radiate in all directions to end in relation to the cells of the greater part of the cortex. Transverse sections (Figs. 119.134 139.) show that a great number cross the middle line, forming a marked decussation. As in the bird the fibres from the inferior olive to the cerebellum terminate in relation to the lateral nucleus (corpus dentatum) to a great extent. ~~(figs.~~)

The <u>cerebello-vestibular tract</u> connects the internal or roof nucleus with the nuclei of the eighth nerve. Experiment has shown that in mammals this tract originates in the internal or roof nucleus, and terminates among the cells of the vestibular nucleus, so that it represents an efferent tract from the cerebellum to the medulla. (Ferrier and Turner). The tract is made up of coarse fibres collected into loose waving bundles, which, in lower mammals, pass round the lateral wall of the fourth ventricle as a broad strand which crosses the fibres of the superior cerebellar peduncle, (Fig. 118) and curves inwards to end in the internal nucleus of the same side to some extent. The greater number of its fibres however form a marked decussation in the ventral part of the cerebellum (Figs. 96. 118, 134, 140.) and enter the opposite nucleus. In man this strand is well marked, though relatively smaller than in such animals as the cat and the rat. In higher forms, where the superior cerebellar peduncle forms a distinct vertical strand in the lateral wall of the fourth ventricle, the inner fibres of the tract pass internal to the peduncle and the more external fibres curve round its outer aspect.

This tract was formerly regarded as the internal part of the restiform body, but is now known by its distinctive title the <u>cerebello-vestibular</u> tract.

The <u>ventral cerebellar tract</u> (Gowers) is a direct continuation from the cord to the cerebellum, but does not join the restiform body. It remains in the antero-lateral part of the medulla until the level of the fifth nerve when it passes

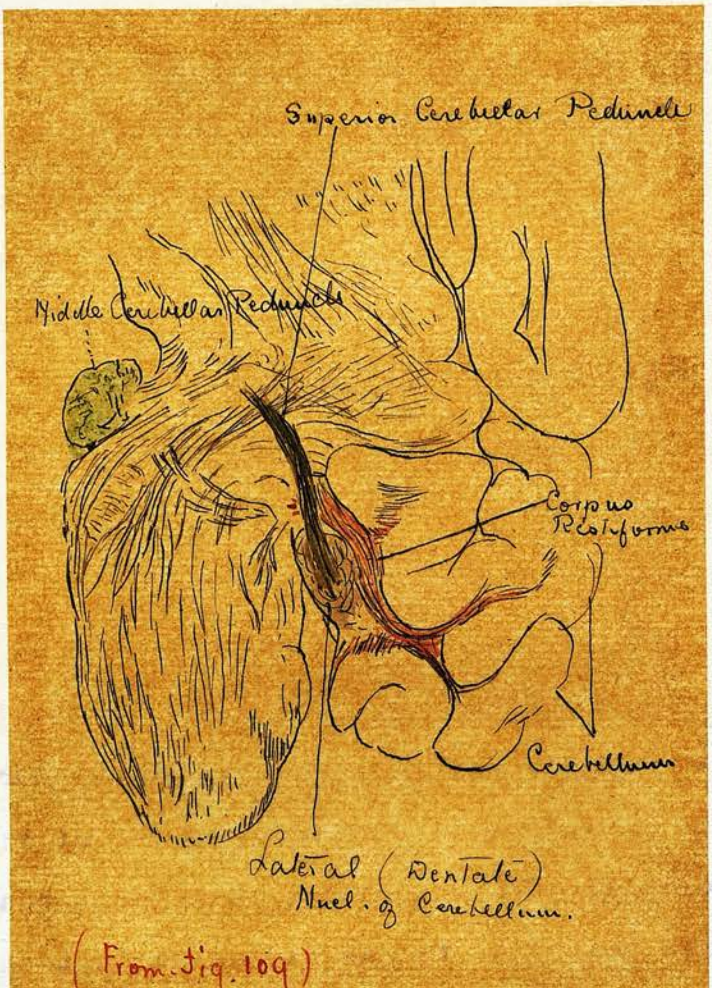


Sagittal section (mole) showing middle and inferior peduncle.

backwards round the outer aspect of the superior cerebellar peduncle to the anterior medullary velum, (the valvula) within which it bends downwards towards the cerebellum. It is analogous to the similar tracts in lower vertebrates.

The middle cerebellar peduncle is a structure peculiar to mammals as far as is known. It has not been described as a distinct formation in any lower vertebrate, although strands have been mentioned as resembling it.

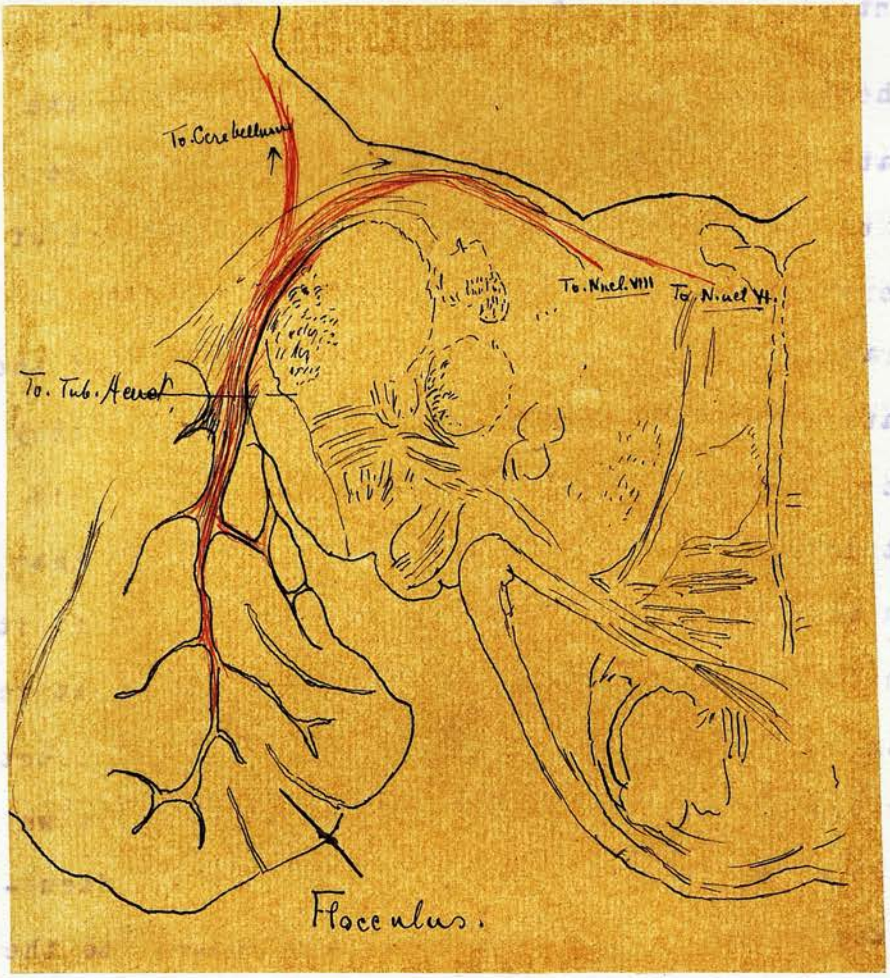
The tract rises in the lateral part of the cerebellum and curves round the periphery of the medulla towards the mesial plane, to end in relation to some scattered nuclei which appear in the ventral portion of the medulla or pons. (Figs. 121. 97) Many of its fibres cross the middle line to terminate in the opposite nuclei, while others end in the nuclei of the same side. A considerable number of fibres bend dorsally into the raphe, some being continued backwards nearly as far as its dorsal extremity. (Fig. 121) Bechterew thinks these fibres pass upwards in the formatio reticularis, but the sections of the opossum seem to show that many of them end in relation to the numerous cells which are present on each side of the raphe at this level. (Fig. 122.) These nuclei within the fibres of the middle cerebellar



Sagittal section (mole) showing Superior Cerebellar Peduncle.

peduncle on the ventral aspect of the medulla seem to be connected with the inferior olive by means of a well-marked bundle of fibres lying in the anterior portion of the medulla. (~~Fig.~~).

The <u>superior cerebellar peduncle</u>, arises in the lateral nucleus, (corpus dentatum) and to some extent also in the cortex of the lateral part of the cerebellum. From these structures the fibres gradually converge towards the dorsal part of the lateral wall of the fourth ventricle, where they bend upwards and form a distinct strand. This structure is very much more distinct in man than in the lower mammals, in which it is less definite in its outline, and more obscured by the relatively larger cerebello-vestibular tract. It is directed obliquely upwards, inwards, and forwards, as is well seen on sagittal sections, (Figs. 100-109) and decussates in the middle line below and ventral to the oculo-motor nuclei (Figs. 107.98). Above this point it is continued upwards for a short distance to end in the nucleus known as the red nucleus, some of its fibres being continued on to the optic thalamus. Many investigators (~~Bechterews~~ Bechterew, Russel, Bruce and others) have shown that this is a composite tract, containing



Scheme of the flocculus and its Connections (Bruce).

fibres from different sources, but it is not necessary to discuss that point here.

The flocculus.

In the higher mammals the most ventral part of the cerebellum at the level of the eighth nerve forms a well marked lobe, known as the flocculus. This lobe is present in the opossum, (Fig. 95) but is small, while in man (fig. 138) it forms a large well-formed portion of the lateral lobe. In the intervening series of mammals it shows gradual development. It differs from the remainder of the cerebellum in the date of medullation of its fibres, which is very early, and in its close relation to the cochlear nucleus of the eighth nerve. As will be seen from figures 95. 138 it lies closely applied to the tuberculum acusticum and sends some fibres into that structure, while others of its fibres curve round the dorsal aspect of the restiform body in such close relation to the fibres from the cochlear nuclei that it is impossible to distinguish them. Bruce has stated that these fibres end in relation to the dorsal nucleus of the eighth nerve, and to the nucleus of the sixth nerve. The flocculus has also intra-cerebellar connections which are not as yet fully known. Thomas traces them to the corpus dentatum and the lateral lobe.

Comparison of the various Types.

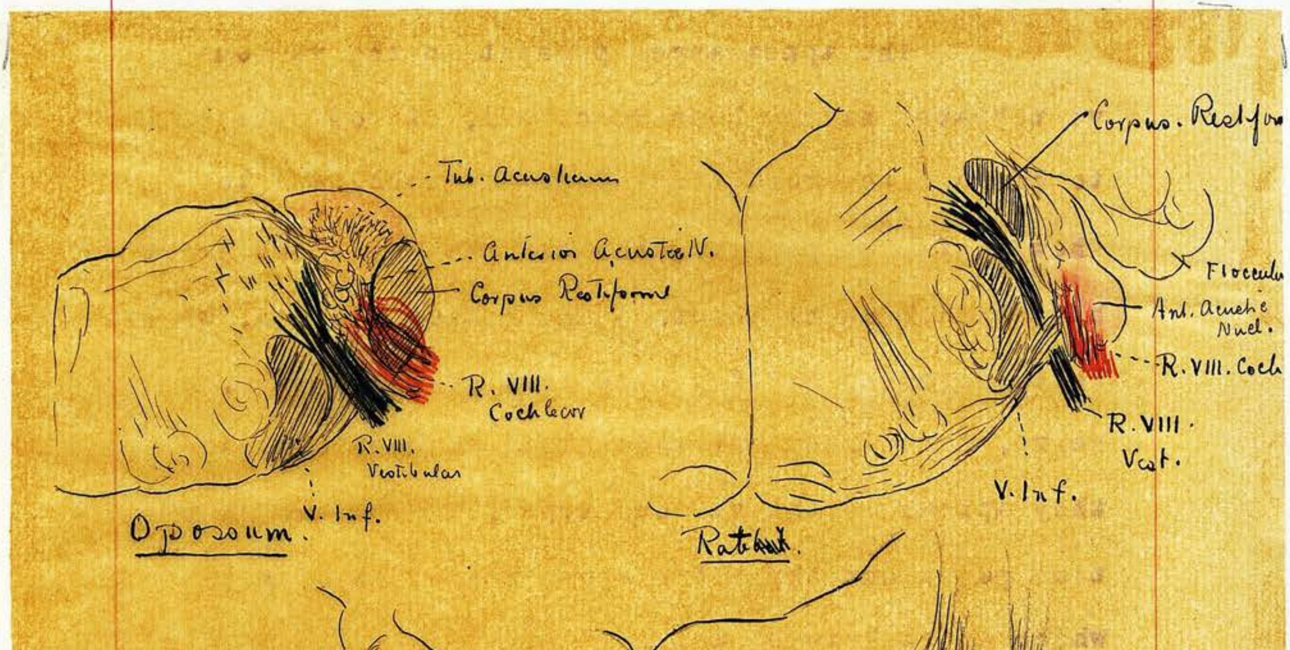
Plates. I – XLIV.

Summary of the results of Examination of typical medullae.

The appearances present in the various vertebrates having been described, it now remains to compare the conditions found in each, and to show as far as possible how the changes which exist have been brought about. The method adopted, will be to describe briefly each part of the system, nerve, nuclei, and intra-cerebral connections, as they appear in the various types, and at the same time point out the differences and relationships which exist between them.

The Eighth Nerve.

The eighth nerve in elasmobranchs consisted of an auditory root and three lateral line roots. In the teleosts there were at least two branches of the auditory root, and the lateral line roots were reduced to two. In the frog the lateral line roots have completely disappeared, while there is a distinct division of the auditory root with a cochlear portion and a vestibular portion. The distinction between the two roots is less marked in the serpent and the vestibular root is smaller in relation to the medulla than it is in the frog. The closer apposition of the roots in the reptile is



Showing the mode of entrance of the auditory roots in various mammals.

probably due to the greater development of the inferior root of the fifth nerve, which pushes the vestibular root backwards.

In birds the root is divided into a distinct cochlear root and a vestibular root, which enter the medulla close together, the cochlear root being much smaller than the other,—the vestibular root enters the medulla in separate small bundles as it did in the skate. Both the roots pierce the corpus restiforme, which runs almost horizontally in the bird. (Figs. 74-77)

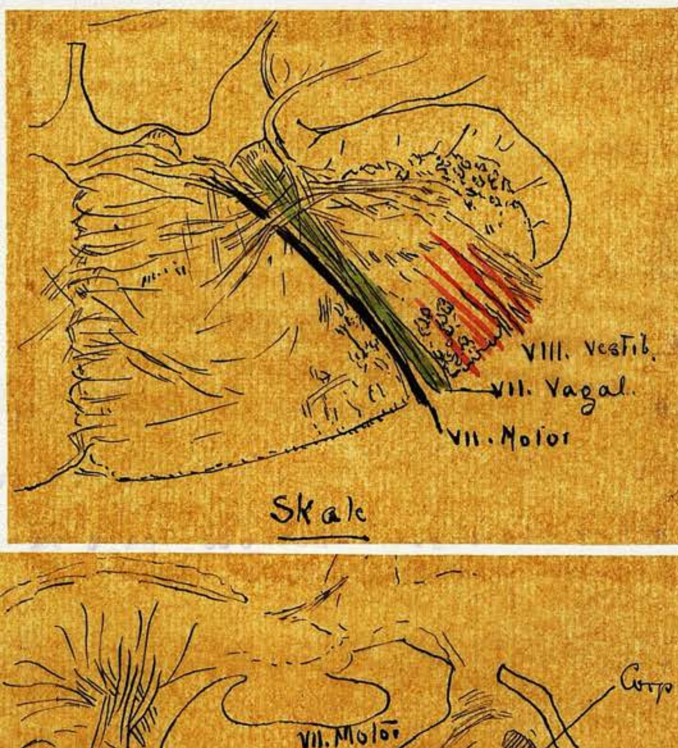
In the opossum the cochlear and vestibular roots are both well marked, the former being the larger. They enter the medulla close together as a series of slightly separated bundles, which pass on the inner side of, or piercing, the restiform body. This latter structure is larger than in birds, and is formed into a strand which, in part of its extent, is longitudinal in direction, so that the auditory nerve roots enter the medulla mainly on its inner side. (Figs. 93-96.).

In the other mammals examined the cochlear and vestibular roots still enter the medulla close together, but in their intra-medullary course they are separated by the restiform body, which has inserted itself between them. They are of nearly equal size in most cases, but the vestibular root has become much more condensed, as already explained, and has to travel some distance into the medulla before reaching its nucleus. This condensation of the root, and removal of the nucleus from the surface, are probably produced by the increased development in mammals of the substantia gelatinosa and the cochlear nuclei as explained on page 116

The fibres of the cochlear root divide into their ascending and descending branches immediately on entering the medulla, and thus, except in the opossum, have almost no intra-cerebral course in the specimens examined.

The root of the seventh nerve is related in position to the roots of the eighth nerve throughout the whole vertebrate series. It consists of two parts, a motor and a sensory. The motor part varies very little in the different types, except in position. In the lower vertebrates it emerges more laterally in the medulla than in the higher forms, and lies immediately ventral to the vestibular root. In the mammals the vestibular nerve is gradually condensed by the increase in size of the substantia gelatinosa, while the facial nerve is displaced to the inner side of that structure. The result is that the two roots

Showing the relations of the motor and vagal roots of the VII. nerve in skate and cat.



Skate

Cat.

become separated from each other by the substantia gelatinosa and the inferior root of the fifth nerve. At the same time the increase in size of the nuclei and nerve tracts in the ventral part of the medulla at the level of the eighth nerve forces the emerging root of the seventh nerve to a higher level in the medulla, and it comes to lie in a higher plane than the eighth roots, although its nucleus continues on the same level. In the higher mammals there is thus a considerable interval between the points of emergence of the roots of the seventh and the eighth nerves.

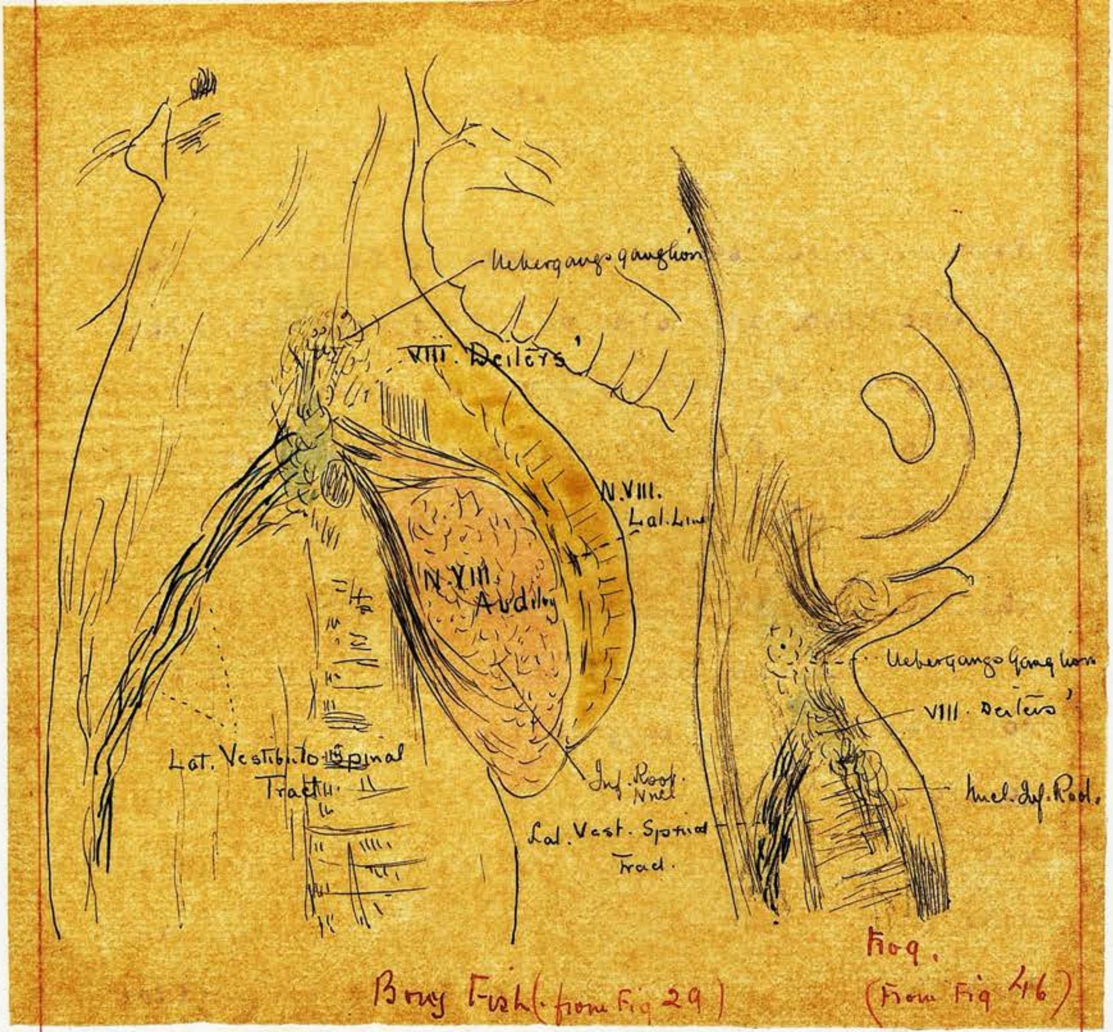
The sensory root of the facial appears in the fishes as a nerve which terminates in the upper end of the vagus nucleus, but which emerges from the medulla on the dorso-lateral aspect of the motor root of the facial nerve, between it and the vestibular nerve. Strong points out that in frogs it ends in the upper end of the fasciculus communis system. In the serpent it has the same origin, but in mammals it appears as a slender nerve, slightly above and internal to the facial root. It terminates in an upward continuation of the nucleus of the fasciculus solitarius. As already said the three structures -

fasciculus solitarius in mammals, fasciculus communis in amphibian, and lobus vagi in fishes - are homologous, and the sensory division of the facial nerve in fishes and frogs is thus homologous with the pars intermedia of Wrisberg in the mammalian medulla.

The nuclei of the eighth nerve.

The nucleus of the eighth nerve in fishes consists of an auditory portion and a lateral line portion. The whole nucleus in the elasmobranchs and ganoids is placed on the lateral aspect of the medulla, as it is also in the higher mammals, this arrangement of parts is owing largely to the fact already stated, that the great development of the cerebellum causes the fourth ventricle to become widened and flattened, and the eighth nucleus thus comes to be in the lateral aspect of the medulla. In the teleosts which have a simpler cerebellum and very large vagal and eighth nuclei, the latter nucleus lies entirely on the dorsal aspect of the medulla, in some species extending over the middle line to fuse with its fellow of the opposite side. (see fig. 23.A).

The auditory portion of the eighth nucleus lies ventral to the lateral line portion in all fishes, and is more dense in structure than the latter. In the



Sagittal sections of teleost and frog showing vestibular nuclei and vestibulo-spinal tract.

elasmobranchs there is no evidence of a division into a cochlear and a vestibular nucleus, but in the teleosts a definite group of cells is present in the upper ventral part of the nucleus and gives origin to the lateral vestibulo-spinal tract. This group of cells is constant in the teleosts and all the higher vertebrates examined. In mammals it is known as Deiters' nucleus. Among the fibres of the inferior eighth root there are many scattered cells in relation to which the fibres of the root terminate. This is best distinguished as the inferior vestibular nucleus. It is not distinctly divided off from Deiters' nucleus. The Uebergangs-ganglion" of Mayser is a nucleus which bears the same relation to the ascending fibres of the eighth nerve (and in part also to similar fibres of the fifth nerve) as the inferior vestibular nucleus bears to the fibres of the inferior root.

These three nuclei, the vestibular nucleus, Deiters' nucleus, and the Uebergangsganglion are not circumscribed groups of cells, but form a chain of irregular groups, extending from the inferior root of the eighth to the level of the junction of the cerebellum and medulla. This is true of the teleosts and elasmobranchs examined, but the specialisation of that part known as Deiters' nucleus is much less marked in elasmobranchs. The classification of the vestibular nucleus is more fully explained on page

The nucleus of the lateral line in fishes lies dorsal to the auditory nucleus. It is of more open texture, containing fewer fibres and is capped by a layer of cerebellar substance. In elasmobranchs and ganoids it consists of two nuclei, a dorsal and a ventral.

The dorsal nucleus or lobus lineae lateralis is separated from the remainder of the nucleus. It has been fully described on (p. 38) The ventral part is in immediate relation to the auditory nucleus proper, lying on its dorsal aspect without any distinct line of demarcation. The teleosts have lost the lobus lineae lateralis and have only the ventral lateral line nucleus.

The nucleus of the eighth nerve in the frog shows for the first time a distinct division into cochlear and vestibular parts. The cochlear nucleus is present as a group of large cells chiefly on the dorsal aspect of the inferior root - the position it maintains in reptiles and birds. There is no trace of a lateral line nucleus, and the inferior vestibular nucleus is not very strongly developed. Deiters' nucleus and the origin of the lateral vestibulo-spinal tract are well seen, but there is only a slight indication of a cerebello-vestibular nucleus. The most evident changes in the transition from the teleost to the frog is thus the increase in the cochlear system, the reduction of the vestibular system and the complete disappearance of the lateral line nerves and nuclei.

The eighth nucleus in reptiles shows a clearly circumscribed cochlear nucleus, placed dorsally in the medulla and receiving the cochlear nerve. It is much more developed than in the frog, and closely resembles in position and appearance the large-celled nucleus of the pigeon.

The vestibular nucleus is relatively small and contains fewer cells than that of other forms; and Deiters' nucleus is much less prominent than in the teleosts, the birds and the human being. The Uebergangsganglion (cerebello-vestibular nucleus) is absent or reduced to very few cells, as in the frog. The increase in the cochlear nucleus is the most marked feature of the reptile medulla.

The eighth nucleus in the bird is very distinctly divided into two parts. It lies dorsally in the

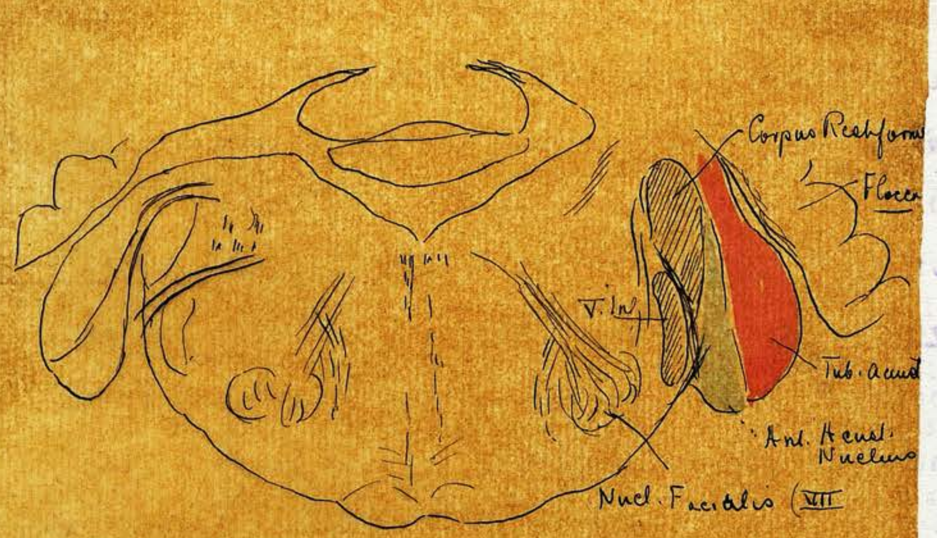
Showing the development of the cochlear and vestibular nuclei.

medulla, as in the reptile, amphibian and bony fish, but is of much greater extent relatively to the size of the medulla than in any of these orders. The cochlear nucleus shows a distinct sub-division into two nuclei, thus foreshadowing the two great cochlear nuclei of mammals, but it differs from the higher mammals in its relation to the medulla, and more especially to the restiform body. In the bird the restiform body is external to the cochlear nucleus, in the higher mammals it is internal. The two cochlear nuclei in the bird, are placed internally and externally in relation to each other, but in mammals the one nucleus lies dorso-lateral to the other, a change in position due to the difference in the relations of the parts of the medulla, and the consequent lateral displacement of the whole nucleus as explained on page

The small celled nucleus is the fore-runner of the tuberculum acusticum of mammals while the large-celled nucleus represents the anterior acustic nucleus. This is indicated by the character of the cells as well as by the relation of the nuclei to each other, and to other parts. The cells of the anterior acustic nucleus are large, round and have few dendrites, and closely resemble those of the large-celled nucleus of birds. The cells of the tuberculum acusticum are small, oval and are placed with their long axis at right angles to the long axis of the nucleus, in some cases forming three layers. The cells of the small-celled nucleus of birds are arranged similarly but are not arranged in a distinctly laminated fashion.

The appearance of a "dorsal" nucleus in birds is a new feature. It is evident that some of the fibres both collaterals and roots of the vestibular nerve end within it, in all birds and mammals. The cochlear root has no direct connection with it. In the birds this nucleus appearance of being a continuation inwards of the smaller cells of the vestibular nucleus, its cells being much smaller than those of the other nuclei. In no case does it deserve the name of "main nucleus", its connection with the root being but slight.

The <u>vestibular nucleus</u> in birds varies in extent with the species. It is very diffuse, and the cells within it being numerous and the specialisation of Deiters' nucleus very marked. The upper extremity of Deiters' nucleus is continued into the <u>cerebello vestibular</u> nucleus of Brandis, a nucleus which lies between the cerebellum and the eighth and fifth nuclei. It is analogous to that known as the "Uebergangsganglion" in the fishes and Bechterew's



Transverse Section (cat) showing Cochlear Nuclei.

nucleus in man. It is of importance to note that the two classes in which this structure is most marked are those in which the greatest demand on the power of equilibration, viz., the bony fishes and the birds, and that further it is always associated with a relatively large vestibular system. In the amphibians, for instance and reptiles this nucleus is absent or very small, and the intracerebral vestibular system is also reduced.

The nuclei of the eighth nerve in mammals vary considerably according to the species attaining their greatest relative size in such amplified forms as the rat, the cat, etc., where quickness of hearing and accurate, rapid movement are necessary. The cochlear part is much more highly developed in proportion than in man, and the vestibular system also is somewhat less in extent in man than in other mammals.

The cochlear nucleus in some mammals, (rodents- in carnivora etc.), is very large as already said. It forms a distinct out-growth on the lateral aspect of the medulla, hidden by the cerebellum in the species in which the lateral lobes of that organ are well developed. In man and monkeys it is less prominent, and almost completely hidden by the large lateral cerebellar lobes. The nucleus is very distinctly divided into two parts, the tuberculum acusticum and the anterior acustic nucleus. Much discussion has been devoted to those two structures, which from their comparatively isolated position and peculiar structure seemed unlike the remainder of the medulla. Some authors (Sala and others) regarded the anterior acustic nucleus as a posterior root ganglion, in part at least, basing their opinion on the peculiar character of the cells within it and the elder His endeavoured to account for it by attributing its origin to a group of cells lying scattered among the fibres of the root outside the medulla in the foetus. It is not necessary however to regard this nucleus as an extra-cerebral structure. The present examination of the auditory nuclei throughout the vertebrate series, puts its intra-cerebral origin beyond doubt. The apparent isolation of the of the position of the cochlear nucleus is due to the re-arrangement of parts rendered necessary by the growth of the restiform body and its interpolation between the vestibular cochlear nuclei, while the peculiarities in the character and arrangement of the cells is fore-shadowed in the bird and the reptile - another important point is that the central connections of the nuclei are to a very great extent the same in mammals as in the lower vertebrates where there is no question as to the intra-medullary nature of the nuclei.

The reversion to the laminated cerebellar type in the arrangement of the cells of the tuberculum acusticum is of great interest, when ~~it is~~ the original close connection of this part of the medulla with the cerebellum is borne in mind.
The close connection between it ans the flocculus also indicates a close relationship between it and the cerebellum, and this resemblance is further borne out by the appearance of a "cortical layer" in the tuberculum acusticum. (Figs. 103-137. 138 & 1c) suggesting the "cerebellar crest" of the fishes.

<u>The central connections of the eighth nerve.</u>

These connections may be divided into two systems:

(a) the connections of the cochlear nuclei.

(b) the connections of the vestibular nuclei, — the former representing the central path for the sense of hearing, the latter the central apparatus for equilibration.

The connections of the cochlear nuclei.

From the cochlear nucleus fibres pass in two main strands in relation to one of the most prominent structures in the lateral part of the medulla,- the inferior root of the fifth nerve. One strand of cochlear fibres passes internal or dorsal to this root and one strand passes ventral to it. In all vertebrates the dorsal strand is present and is known in mammals as the striae medullares, a name which will be applied to the analogous fibres in all vertebrates. The ventral strand is much more variable in size, and apparently may even be absent altogether, as in the serpent. When present it is known as the corpus trapezoideum. The relative size of these two tracts is apparently determined less by the size than by the position of the cochlear nuclei. When these nuclei, or nucleus in lower forms, is placed dorsally and near the middle line as in the bony fish, the serpent, and the bird (see ~~diagram~~ Figs. 27-57-73) the striae medullares form a large strand while the corpus trapezoideum is small or absent. On the other hand when the medulla is flattened out by the shallowness and width of the fourth ventricle and the cochlear nucleus is thus placed more laterally, as in the skate, the frog and the mammals, the corpus trapezoideum increases in size, while the striae medullares diminishes. The condition found in the opossum is interesting in this connection, since it shows a transition stage between the bird and the mammal. In the opossum the cochlear nuclei are not so laterally placed in the medulla as in higher mammals and the result is that the great majority of the fibres pass dorsal to the fifth nerve, and form striae medullares, while the smaller portion goes to form the corpus trapezoideum. In higher mammals this condition is reversed, while in birds the striae medullares are very large and there is only an exceedingly small corpus trapezoideum. It would seem from this that the fibres of the nuclei of the auditory nerve preserve the faculty observed by Miss Platt in the peripheral fibres of the related lateral line nerve - they travel to their centres along the lines of least resistance, taking the shortest and easiest path to their point of termination. Their relation to the inferior root of the fifth nerve is determined by the fact that this structure is an earlier formation than the cochlear nuclei, and is interposed between the latter and the remainder of the medulla. The fibres from the cochlear nuclei must therefore pass round the inferior root of the fifth nerve on one or other of its aspects in order to follow out their central paths. This division of the fibres results in the formation of the dorsal path, the striae medullares and striae acusticae, and the ventral path, the corpus trapezoideum.

The striae medullares.

This tract in all vertebrates below man includes all the fibres which pass from the cochlear nucleus internal or dorsal to the inferior roots of the fifth nerve, and may be regarded as the dorsal auditory tract. It is composed in the elasmobranchs of fibres which pass towards the superior olive of the same and of the opposite sides, in which some of the fibres end while others turn upwards into the lateral fillet. In the skate the fibres from the lateral line nucleus and the auditory nucleus are not clearly distinguishable, but that a certain number of the arcuate fibres pursue this course is evident. The fibres to the opposite fillet are well marked.

In the teleost the presence of the arcuate fibres from the lateral line nucleus also obscures the relations of the system, but it is known that a large strand of fibres enters the lateral longitudinal bundle of Mayser, and pass upwards to end in the structure which is the analogue of the corpus quadrigeminum in man. This strand in its course from the auditory nucleus to the lateral longitudinal bundle would thus represent the striae medullares of other forms.

In the frog, where the lateral line system is absent, the conditions are much simpler. The striae medullares are seen as a bundle of fibres passing ventrally and inwards from the cochlear nucleus, the majority of the fibres going towards the opposite superior olive and a few to the olive of the same side. This strand is comparatively small in the frog, but the corpus trapezoideum, as said above, is relatively large.

The striae medullares of the serpent are more marked than those of the frog, but their terminations are the same. The increase in size is due not only to the increase in the cochlear nucleus, but also to the fact that there is no corpus trapezoideum in the serpent, and that the striae therefore represent the only central auditory path.

In birds the presence of a double cochlear nucleus, increases the complexity of the striae medullares which in this class contain fibres which pass:

(1) From the large-celled nucleus to both superior olives.

(2) From the large celled nucleus to the opposite lateral fillet.

(3) From the small-celled nucleus to the opposite cochlear nucleus.

(4) From the small-celled nucleus to the superior olive of both sides and probably to the lateral fillet.

In the bird, and in the serpent, the striae medullares are well-marked, and the corpus trapezoideum is small or wanting. In the mammals there is a gradual diminution in the size of the striae in inverse proportion to the gradual increase of the corpus trapezoideum, as will at once be seen if the medullae of the opossum, the calf, the mouse, the cat and man be compared. The method of this gradual transference will be explained in dealing with the corpus trapezoideum. The striae in lower mammals consist of:-

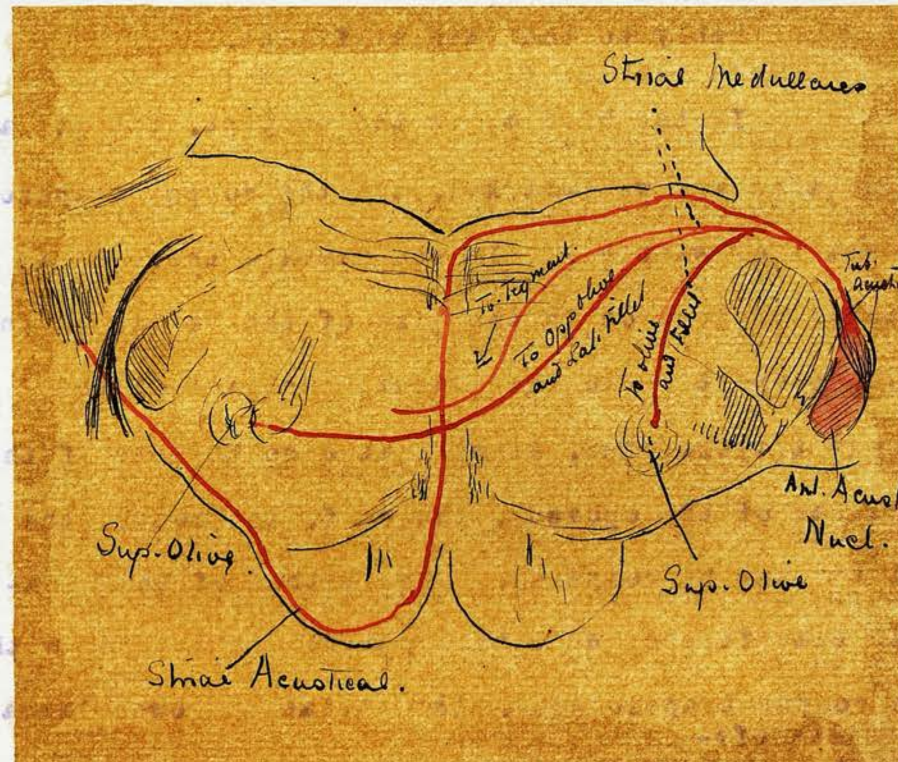
1. Fibres from the anterior acustic nucleus to:-

(a) The superior olive its accessory nuclei and the lateral fillet of the same side.

(b) " " " " opposite side.

(c) Probably to the median fillet of the opposite side.

(d) the tegment of the opposite side. (Kölliker).



Scheme, Showing connections, (dorsal) of auditory nuclei in man, consisting of Striae Acusticae and Striae medullares.

2. Fibres from the tuberculum acusticum to:-

   (a) the superior olive and its accessory nuclei and to the lateral fillet of the same side.

   (b) the corresponding structures on the opposite side.

   (c) The median fillet of the opposite side (?)

   (d) the tegment of the opposite side (?) (Kölliker)

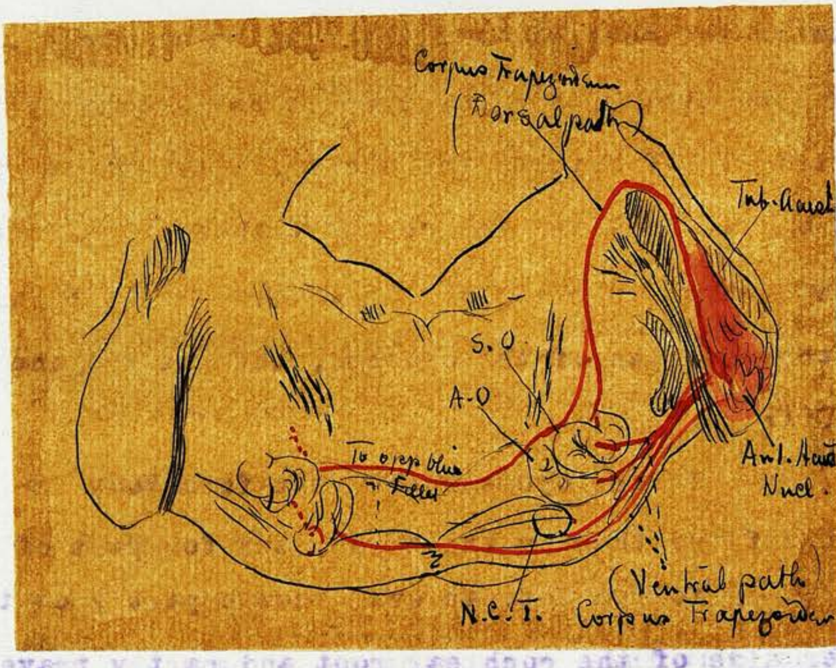
In man the first series of fibres is unrepresented since, as will be seen, they travel by way of the corpus trapezoideum. An additional strand, the striae acusticae from the cochlear nuclei to the opposite restiform body is described as present in man by Kölliker (see P.131), but is absent in lower forms. The striae medullares therefore are present throughout the whole vertebrate series, varying in extent with the size of the cochlea and the development of the corpus trapezoideum.

The corpus trapezoideum or ventral auditory tract is seen in the greatest perfection, amongst the classes examined, in the cat and the rabbit, where it forms a broad band stretching from side to side of the medulla between the two cochlear nuclei. It is composed entirely of fibres derived from these nuclei, and from the nuclei which lie among its fibres, viz., the superior olive, and, when present, the accessory olive, nucleus pre-olivaris and nucleus of the trapezoid body.

In the lower vertebrates the corpus trapezoideum is represented by fibres which emerge from the lateral aspect of the auditory nucleus, or from the cochlear nucleus when this is present, and pass round the outer side of the inferior root of the fifth nerve towards the superior olive. Here they either terminate or bend upwards into the lateral fillet.

These fibres are present in considerable numbers in elasmobranchs, but are not numerous in teleosts. In the frog they are again well represented, but in the serpent they are completely absent, and in the bird they are very few in number. As has already been said, their presence probably depends less on the size of the cochlear nucleus than on its position. When the nucleus is placed laterally in the medulla, its fibres pass mainly or entirely ventral to the fifth nerve, and form the corpus trapezoideum. When placed more dorsally the fibres find their way by the internal aspect of the fifth nerve and form the striae medullares. In mammals the greater number of the fibres from the auditory nuclei travel by way of the corpus trapezoideum, until in the higher mammals, and especially in man, the striae medullares are relatively very small. In the lower mammal examined, the number of fibres which pass round the dorsal aspect of the inferior root is very great, probably the majority of the auditory fibres take this path, but the corpus trapezoideum is also of considerable size. In mammals the course of these fibres is further interrupted by the intrusion among them of a new strand - the corpus restiforme. This strand, which in birds passed obliquely backwards and upwards, entirely on the external aspect of the auditory nuclei, appears in the higher mammals wedged in between the cochlear and the vestibular nuclei. In order to attain this position it has gradually inserted itself between the nuclei, altering its relations to them and the corpus trapezoideum in a manner which is clearly illustrated in the figures of the medullae of the opossum, the rat and the cat, (~~Figs.~~ Plates XXIX. XXIV. XXXIX.).

In the opossum the restiform body is more defined than in the birds, and for part of its course is formed into an oval bundle partly on the outer side of the cochlear root and partly traversed by its fibres. In the calf this bundle is found



Scheme of Corpus Trapezoideum in the Cat.

on the inner side of the cochlear root, and of the cochlear nucleus. To attain this position the restiform body must cross the fibres of the cochlear root and the corpus trapezoideum. This it does by gradually inserting itself between the fibres of the latter structures, so that at first a few fibres, later the greater part, and finally all the fibres of the cochlear root are displaced to the outer side of the restiform body, while the corpus trapezoideum is displaced to its ventral aspect. Reference to the accompanying Figures (in Plates 29-39-40) ~~diagrams~~ will explain this process, which was originally suggested by Held, as occuring in the development of the rabbit's medulla, but which is now seen also to take place in the evolution of the vertebrate medulla. The "dorsal path" of Held is seen during a stage of this process, at a time when part of the corpus trapezoideum still lies dorsal to the restiform body. Held states that it merely represents a part of the former tract, which joins the main body after curving round the corpus restiforme. The appearance present in the opossum's medulla suggest that this dorsal path is not, as commonly said, derived entirely from the anterior acustic nucleus, but that it originates in part, in this form at least, from the tuberculum acusticum also.

<u>The secondary nuclei of the auditory tract.</u> The fibres of the corpus trapezoideum and some of the striae medullares are brought together in relation to certain nuclei in the ventral portion of the upper medulla. These nuclei, in the mammals in which the auditory system is most perfect, are four in number:-

1. The superior olive.
2. The accessory olive.
3. The nucleus praeolivaris (Cajal).
4. The nucleus of the corpus trapezoideum (Held).

They have already been fully described (Cajal, Kölliker) as they are seen in the mouse, the rat and the cat, (page 129) and their development in the vertebrate series will now be considered.

In the skate, a few cells scattered in the lateral region of the upper medulla, in relation to the arcuate fibres which represent the corpus trapezoideum, take the place of the future superior olive. In the teleosts a group of large cells accompanying the lateral longitudinal bundle bear a close relation to the dense strand of arcuate fibres from the eighth nucleus, and are probably analogous to the olive. In the frog there is a distinct group of cells which lies in relation to the lateral fillet when that tract begins to be formed and which is continued without interruption into the mid-brain as the lateral fillet nucleus. In the reptile this group of cells is larger, and continued upwards until the lateral fillet merges in the posterior corpus quadrigeminum. In birds the cells constitute a distinct nucleus, which appears as the lateral fillet is formed, and accompanies it upwards until the nucleus is merged in the terminal nucleus of the fillet. Bruce has stated that in man the lateral fillet nucleus is the upward continuation of the superior olive and this statement is borne out by the conditions found in the lower vertebrates and described here.

In mammals the superior olive begins to assume larger proportions. In the opossum, the rat, the mole and the calf it is a distinct rounded nucleus, in the rat it is slightly convoluted. In man the superior olive is a simpler structure than in the cat or rabbit, consisting of a rounded nucleus with in some cases, a tendency to a convoluted outline. The appearances in these types are shown in the accompanying diagram. (p. 129)

The accessory olive is only seen in mammals, and varies considerably in the various orders. It is largest in the animals in which the superior olive is well-formed, and appears to be a very important member of this group of nuclei. The peduncle of the olive rises largely from it in cases where it is well marked, and many of the fibres of the corpus trapezoideum and striae medullares end in relation to it.

The <u>nucleus preolivaris</u> (Fig.127) was described by Cajal who first observed it in the mouse. Its most important feature is its connection with a large bundle of collaterals from the corpus trapezoideum (fig.134) which enter it and terminate partly among its cells, and partly among those of the superior olive. These are specially well seen in the calf (fig. 134), but are present to some extent in all the mammals examined.

The <u>nucleus of the corpus trapezoideum</u> is a structure which appears first as a small group of cells near the superior olive in the bird. It is present in all mammals increasing in size as the corpus trapezoideum becomes more highly developed.

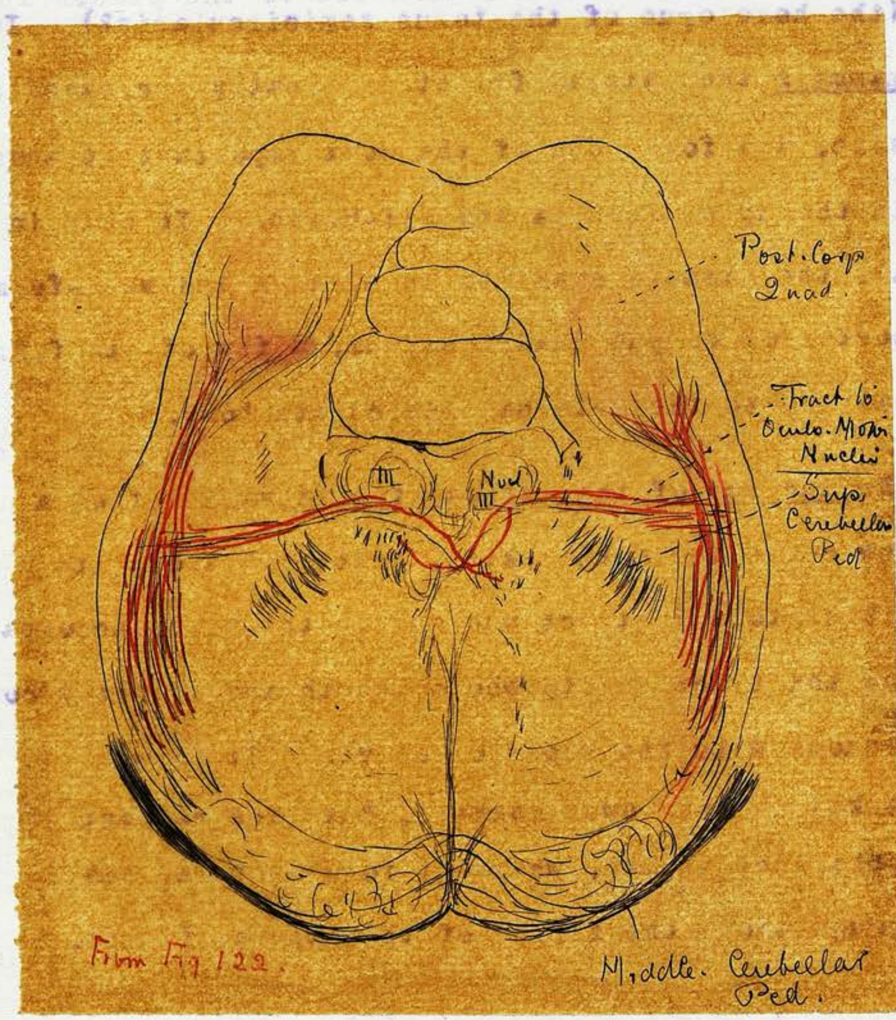
Its minute structure has been very fully described by Cajal and Held, but its connections are still obscure. All that can be said definitely is that it receives fibres from, and gives fibres to, the corpus trapezoideum.

The <u>lateral fillet</u>.

This tract forms the central path for the sense of hearing and connects the auditory nuclei, and the secondary auditory nuclei, with the corpus quadrigeminum or the analogous nuclei. In all classes, except the teleostean, it lies in the lateral part of the medulla and passes upwards and backwards towards the mid-brain, where it terminates. Turner has traced some of its fibres into the internal geniculate body. The nucleus in which it terminates, although of very varying appearance in the different types, is invariable in two points. It is always in the mid-brain and always in close relation to the nuclei of the <u>optic lobe</u> or in mammals, the <u>anterior corpus quadrigeminum</u>.

In the skate the lateral fillet runs in the lateral part of the medulla and terminates in the lower part of the optic lobe. In the teleosts the lateral longitudinal bundle represents the lateral fillet, and passes upwards to end in the torus semicircularis of the optic lobe. In the frog the fillet is in the lateral part of the medulla and ends in relation to a nucleus at the lower part of the optic lobe, evidently homologous with the torus semicircularis. In the <u>serpent</u>, the tract lies in its usual position, but ends in a structure now seen for the first time, the posterior corpus quadrigeminum. This body contains a nucleus, the homologue of the torus semi-circularis of the fishes and the frog, in which the fillet ends. In the birds the corpus quadrigeminum has disappeared, and the lateral fillet ends partly in a small nucleus which lies at the inner and lower part of the optic lobe and partly in the ganglion laterale mesencephali, (the homologue of the torus semicircularis?) In mammals the lateral fillet is greatly increased in size, and forms one of the most important strands in the upper medulla and mid-brain. It ends, in all the mammals examined, in a large and well-formed posterior corpus quadrigeminum, a few of its fibres passing to the internal geniculate body.

The nucleus of the lateral fillet varies from a few cells as in the skate, scattered among its fibres, to a distinct nucleus in the bird, accompanying the tract in its whole length and directly continuous with the superior olive. It is well marked in the lower mammals, but less compact in appearance in man, where it forms several small groups among the fibres of the lateral fillet.



Transverse section (rat) showing tract from the lateral fillet to the oculo motor nuclei

Connections of the lateral fillet nucleus.

A tract connecting the upper end of the lateral fillet with the arcuate system at the level of the oculo-motor nuclei was figured by Bruce and subsequently described by Kölliker, who states that it passes into the arcuate system and decussates dorsal to the decussation of the superior cerebellar peduncle.

The examination of the medullae of the pigeon and the opossum proves that this tract is merely the upper portion of a continuous series of fibres, which begins as the strand from the superior olive towards the grey matter of the floor of the fourth ventricle and the sixth nucleus (the peduncle of the olive). The fibres continue to pass in towards the floor of the fourth ventricle throughout the whole extent of the nucleus but at the level of the fourth and third nerves it is greatly increased in size. Some of its fibres terminate in relation to the grey matter near these nuclei, some directly enter the oculo-motor nuclei of the same side, and some cross the raphe. Those which cross the middle line end partly in the opposite oculo-motor nuclei, partly in the formatio reticularis, where they are lost. This tract in certain classes, forms an important connection between the cochlear nuclei and the oculo-motor nuclei. It is present in man but not so well marked as in the opossum the rat or the rabbit. The oculo-motor nuclei are thus acted upon both by the vestibular nerve and by the cochlear nerve. The former connection travels from Deiters' nucleus by way of the posterior longitudinal fasciculus and the latter from the cochlear nuclei by way of the lateral fillet.

Scheme of Vestibular nuclei in man.

The vestibular nuclei and their connections.

This system undergoes less modification than the cochlear system during the evolution of the vertebrates from the fishes to man, and forms one of the most permanent and invariable systems of the medulla, easily recognisable by reason of the conspicuous character of some of its cells and fibres.

The vestibular nuclei may be regarded ~~as~~ as two nuclei, an internal and an external, subdivided into four main parts, three of which exist in all vertebrates, and the fourth only in the birds and mammals. The four parts as they appear in man are as follows.

External

1. Deiters' nucleus. The cells of Müllers fibres" in the fish & the frog. Un-named but present in birds and reptiles..
2. Bechterew's nucleus. The Uebergangsganglion in fishes; a small un-named nucleus in the frog and serpent, the "nucleus cerebello-vestibularis" of birds.
3. The nucleus of the inferior root, known as such in all vertebrates.

Internal

4. The dorsal or main nucleus. Only present in birds and mammals.

Following the suggestion of Bruce and Kölliker these nuclei might now be termed the superior, middle and inferior external vestibular nucleus, and the internal vestibular nucleus.

Deiters' nucleus is present in all vertebrates as large multipolar cells in the upper and ventral portion of the vestibular nucleus.

Bechterew's nucleus, or the superior external vestibular nucleus is analogous to the "nucleus cerebello vestibularis" of birds, and to the "Uebergangsganglion" of fishes. It is present, as yet un-named in the frog and serpent as scattered cells at the base of the cerebellum. In fishes it is very large, and in birds and lower mammals it is also of considerable size but in amphibia and reptiles and man, it is only a small group of cells. It thus varies in inverse ratio to the size of the cerebellum.

The nucleus of the inferior root or inferior external vestibular nucleus, is formed by the cells which lie scattered among the fibres of the inferior root. It is present in all vertebrates in the same position and showing the same character of cells, viz., multipolar cells of all sizes and shapes. It is almost continuous below with the nucleus cuneatus.

The dorsal nucleus appears in birds as a distinct component of the group of vestibular nuclei. In birds it begins below in close relation to the inferior root of the eighth nerve, lying on its inner aspect, and accompanying it throughout its extent. In mammals it occupies the same position, but seems to send a prolongation downwards between the nuclei of the hypoglossal and the vagus nuclei,- the nucleus intercalatus of Sala. It differs from the other nuclei in appearance, being pale grey and consisting of numerous small cells with a dense network of very fine fibres about them. It is stated that some of the vestibular roots enter this nucleus (Bruce, Kölliker, Cajal, Obersteiner), certainly many fine fibres, both root fibres and collaterals, from the inferior vestibular root end among the cells of the dorsal nucleus.

From what has just been said it will be seen that the vestibular nucleus is fairly constant in its appearance among the vertebrates, the most marked variation being in the size of the superior nucleus, (which as already said varies in inverse ratio to the size of the cerebellum), and the appearance in birds and mammals of an internal nucleus.

The connection of the lateral line nucleus with the vestibular nucleus has been shown (p. 121).
This nucleus is only present in the fishes and some amphibians:- in the teleosts as a dorsal portion of the common "acustico-lateral" nucleus;- in the

elasmobranchs and ganoids as two nuclei, a ventral nucleus similar to that of the teleosts, and a dorsal nucleus, the lobus lineae lateralis. In those amphibia, in which it is present the nucleus bears the same relation to the nucleus of the eighth nerve as in teleosts.

The intra-cerebral connections of the vestibular part of the eighth nucleus are also practically constant throughout the vertebrate series. They are as follows:-

1. The fibres from Deiters' nucleus to the posterior longitudinal fasciculus of both sides.
2. The fibres from Deiters' nucleus to the antero-lateral column of the cord.
3. The fibres from Deiters' nucleus, the dorsal nucleus and the inferior root to the opposite median fillet (Bruce) and to the opposite tegment (Kölliker).
4. The cerebello-vestibular tract.

The first two tracts have been repeatedly described, and their existence in all the vertebrates examined is beyond doubt. They were known in the petromyzon (Ahlborn) The teleost (Mayser) and the frog (Köppen) as Müllers fibres. They have been illustrated here in the serpent and the birds.

(Wallenberg's experiment has proved beyond question their existence in the pigeon). Their presence in the various mammals has been demonstrated here and elsewhere, and has been figured by Bruce, Kölliker, Risien Russel and Thomas in the human foetus. They were easily distinguished in all the vertebrates examined for this thesis. In some cases where the formatio reticularis was greatly beset with fibres, it was not easy to trace them in transverse sections, but in such cases they were found in the longitudinal sections.

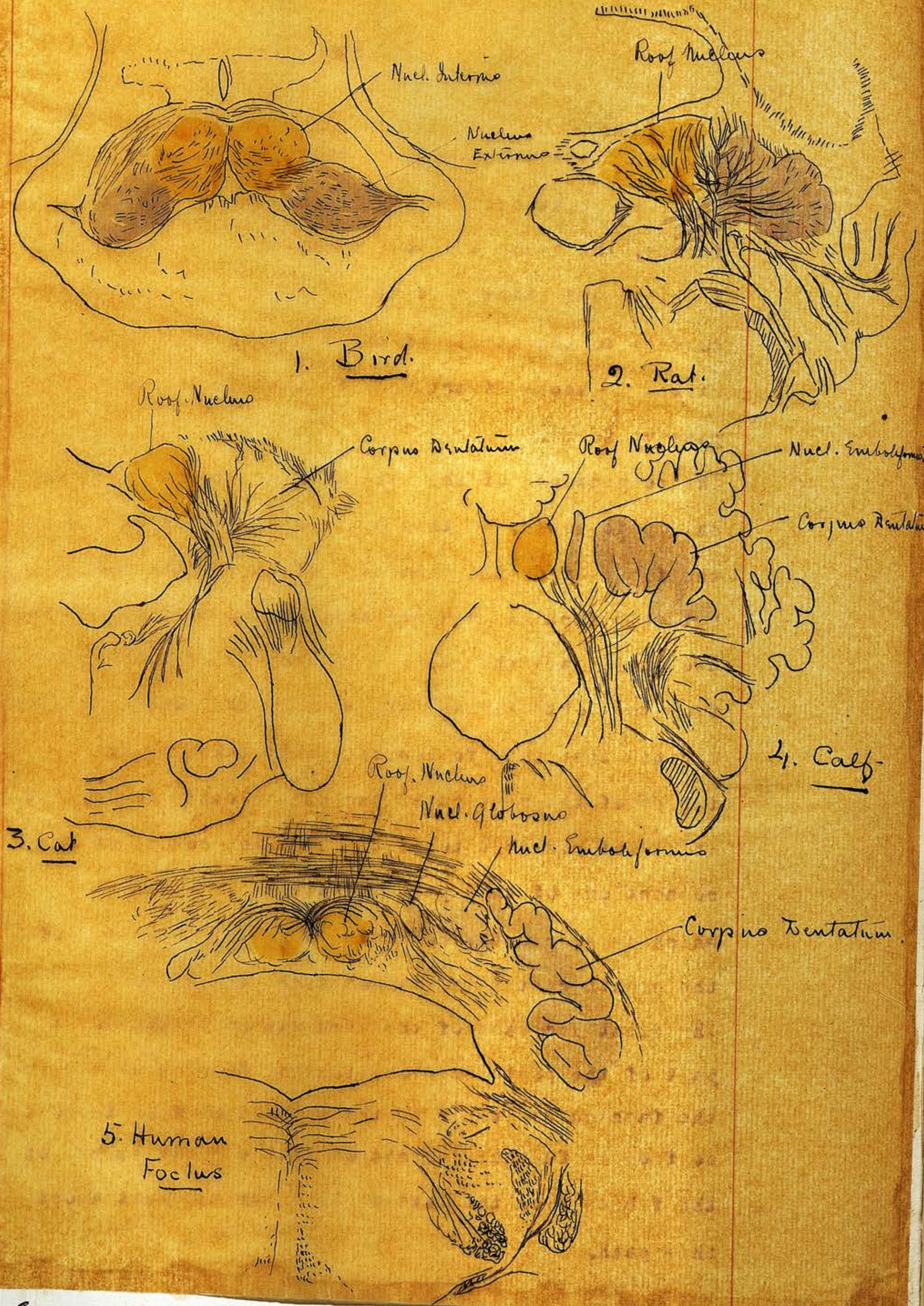
The portion of ~~the part of~~ this tract which enters into connection with the oculo-motor nuclei could not be definitely determined in lower forms, but Wallenberg found it degenerated in the pigeon, after injury to Deiters' nucleus, and it has been proved experimentally to exist in several of the mammals,—the dog, the cat, the monkey etc.,, by Thomas, Ferrier and Turner, Risien Russel and others.

As there is little or no variation in these tracts in the different vertebrates there is no necessity for tracing them through the series. Any change which may occur in them is merely one of size. The tracts are small in the classes in which there is no great demand for an elaborate equilibrating mechanism, as in the amphibia, and the reptiles, but well marked in those in which the mode of life requires great equilibrating power as in the bony fishes, the birds and some mammals.

In birds and mammals it varies greatly in extent according to the habits of the animals, being better marked in those of active life than in the more passive forms.

The connections of the lateral line nucleus are not easily followed, as they are closely associated with the fibres from the remainder of the eighth nucleus, but this fact is evidence that the connections of the two nuclei are the same. The course of the fibres from the lobus lineae lateralis in the skate indicates that they follow the paths taken by the fibres of the vestibular nucleus in other forms, but as said, it is not possible to distinguish the course of the connections of that part of lateral line nucleus which is so closely connected with the remainder of the eighth centre in elasmobranchs and teleosts.

The great decrease of the decussation in the dorsal part of the posterior longitudinal fasciculus and in the fasciculus itself in the transition from teleost to frog is further indication that a great number of the fibres from the lateral line nucleus must adopt this path.

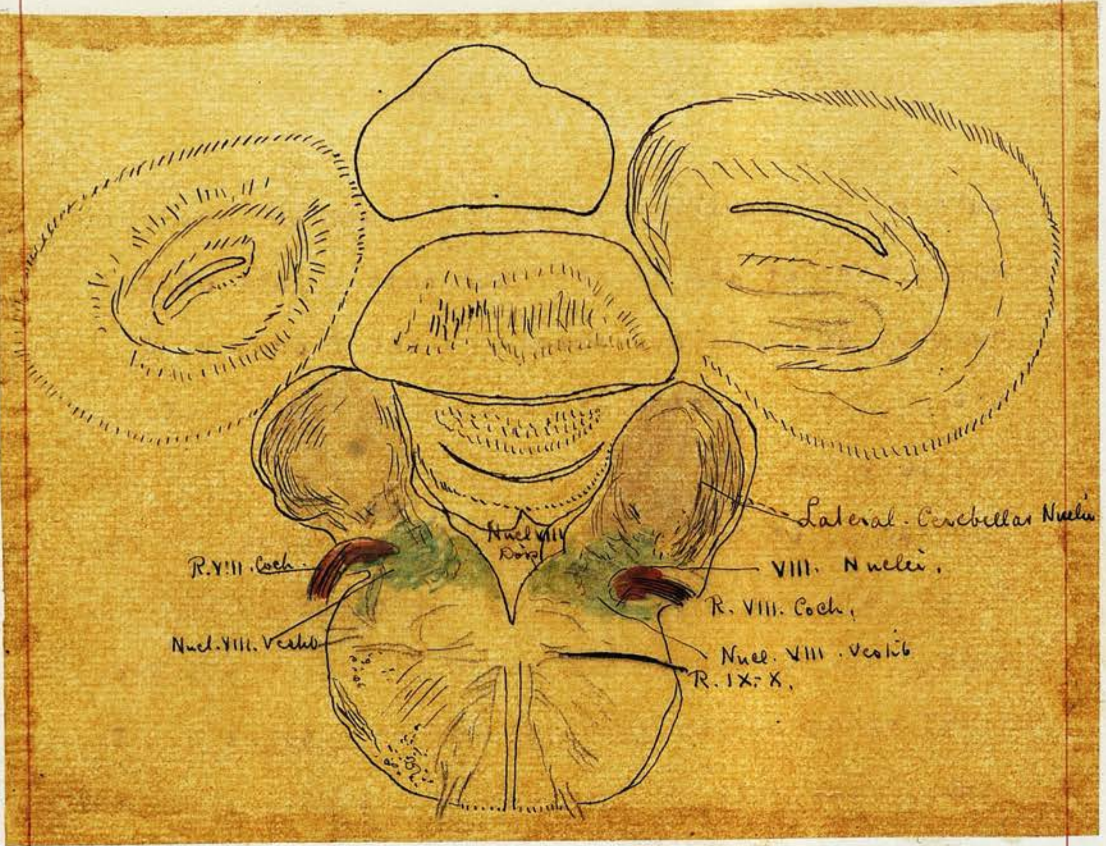


Showing the development of the nuclei of the cerebellum.

The cerebellum and its connections.

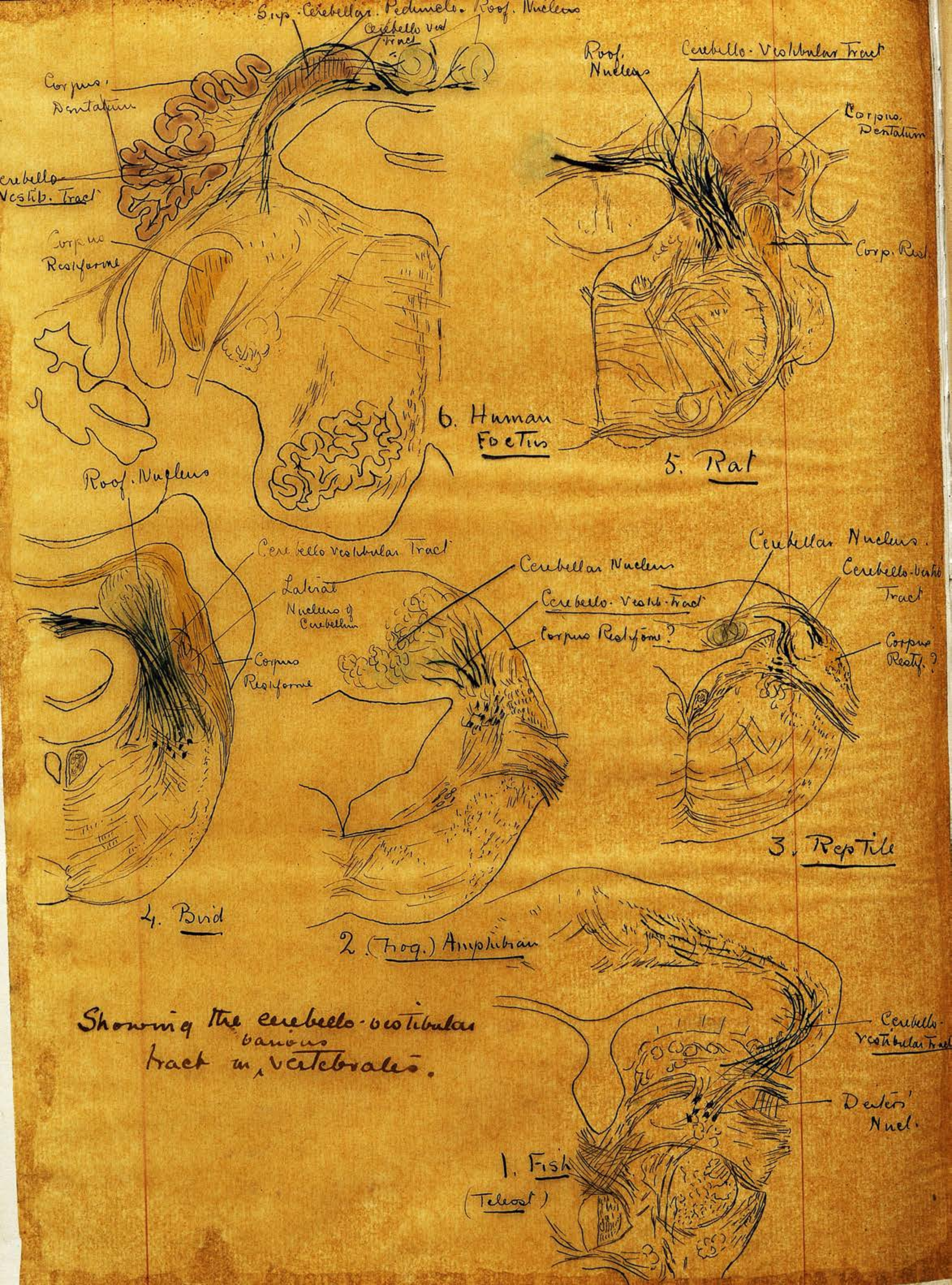
The close association of the eighth nuclei and the cerebellum in the fishes has been recently pointed out by Johnstone, and Bennet Stroud in his work on the mammalian cerebellum proves that the latter structure is formed by a backward growth from the lateral wall of the medulla in the region of the auditory centre. The cerebellum would thus represent a secondary out-growth from the auditory nuclei, which passes backwards, fuses in the middle line, and, as it develops further, assumes the characteristic plicated arrangement of this organ. Its growth thus closely resembles that of the other dorsal nuclei of the medulla and mid-brain. It has been seen that the lobus vagi, the so-called lobus trigemini and the auditory nucleus, when highly developed, extend backwards and fuse in the middle line, and that the same process occurs in the posterior corpus quadrigeminum and optic lobes. There is no doubt that this mode of growth takes place in the cerebellum and therefore its close connection with the eighth nucleus is easily explicable. Further proof of this connection is found in the following facts:- the eighth nucleus in fishes and some amphibia is covered by a layer of true cerebellar substance:- that one of the auditory nuclei in the mammals, the tuberculum acusticum tends, to resume the laminated appearance of the cerebellum: that a lobe of the cerebellum in higher mammals - the flocculus - enters into direct connection with several of the auditory nuclei.

The nuclei of the cerebellum do not appear in the fishes and are only slightly indicated in the amphibians and reptiles. In birds there are two distinct nuclei an internal and an external. In mammals the external nucleus increases in size and gradually becomes convoluted until in man it appears as a repeatedly convoluted body, the corpus dentatum. The internal or roof nucleus, on the other hand, tends to grow relatively smaller and more compact in the higher forms, and, at the same time, to approach the middle line, until in man the two roof nuclei are placed almost close together in the upper and ventral part of the cerebellum which forms roof of the fourth ventricle. Two smaller nuclei appear in the higher mammals, the nucleus globosus and the nucleus emboliformis, but these are now regarded not as separate nuclei, but as small sub-divisions of the corpus dentatum which have been cut off from the main nucleus by the passage of strands of fibres through it.



Frontal section (pigeon) showing close relation between cerebellar and vestibular nuclei.

In the bird and the lower mammals these nuclei are not sharply divided from each other or form the upper division of the vestibular nucleus. This relationship, which is very evident in birds, was recognised by Brandis, and is shown in the accompanying illustration, not only in the bird, but in such mammals as the opossum, the mole and the rat. In the cat the nuclei are much more distinctly separated, while in the calf the smaller nuclei have begun to appear, although much less evident than in man. (see opp. page 176 diagram). These facts tend to support the view that the cerebellar nuclei are developed from the auditory nucleus, and become specialised in proportion to the increased importance and number of the afferent and efferent tracts which connect the cerebellum with other parts. It is interesting in this connection to note that the lateral nucleus increases greatly in size and importance in higher mammals in proportion to the development of the inferior olivary tract, the middle and superior cerebellar peduncles, all these structures being in connection with the lateral lobes and lateral nucleus. On the other hand the roof nucleus tends to become relatively smaller, a fact which may be explained by the diminution in size of the cerebello-vestibular tract, The

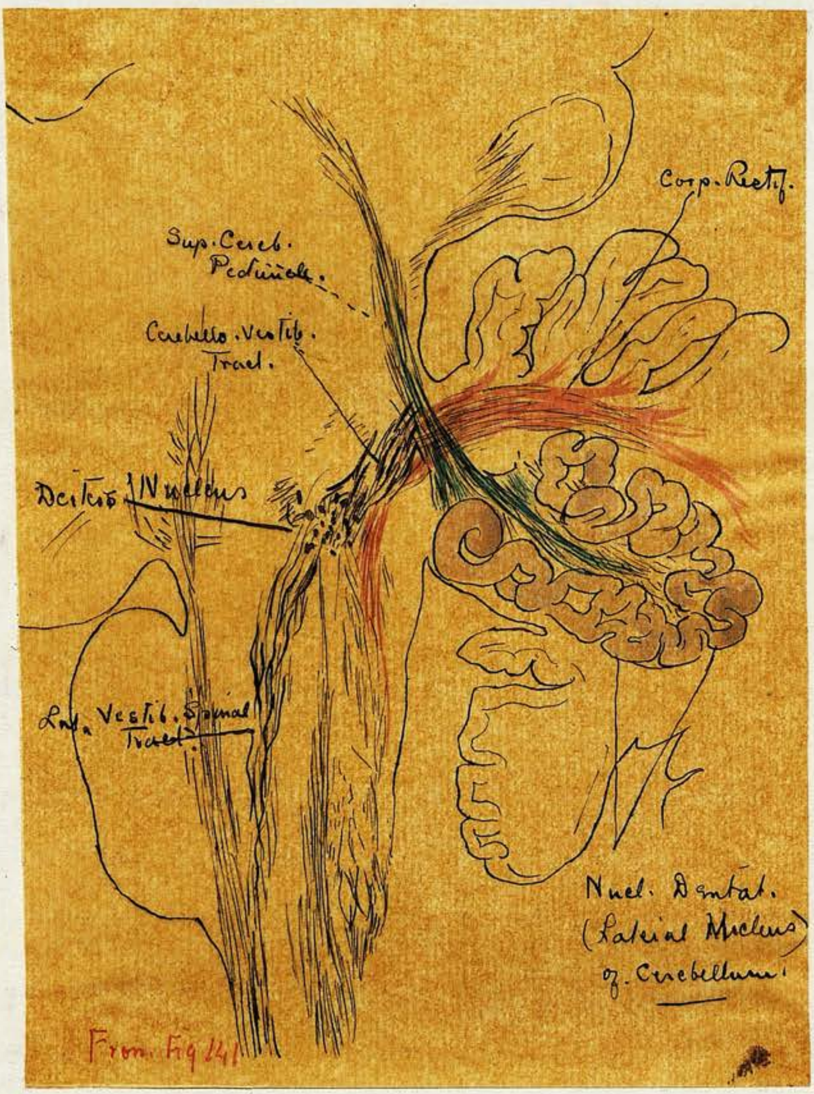


Showing the cerebello-vestibular tract in various vertebrates.

corpus restiforme in the birds and higher vertebrates upwards maintains much the same relative proportion in all the medullae examined. Unfortunately there were no medullae available for examination which showed a transition stage between the fully-formed cerebellar nuclei of the bird, and the very rudimentary nucleus of the reptile, so that no absolute conclusions as to the derivation of the cerebellar nuclei from the eighth nuclei can be drawn, although such a view is strongly suggested.

The cerebellar connections vary greatly throughout the vertebrate series, and will be discussed briefly here.

The most important as regards the present thesis is the cerebello-vestibular tract, and if this is accepted broadly as the tract between the superior external vestibular nucleus and the cerebellum, it may be said to be invariably present in all vertebrates, although it is only in the birds and mammals that it appears as a well-defined tract. In lower vertebrates it is diffuse and ill-defined. In the fish it is formed by the fibres between the cerebello-vestibular, eighth, and fifth nuclei to the cortex of the cerebellum, and in the amphibian and reptiles it extends between these nuclei and


Sup. Cereb. Peduncle.
Cerebello. Vestib. Tract.
Corp. Restif.
Deiters' Nucleus
Lat. Vestib. Spinal Tract.
Nucl. Dentat. (Lateral Nucleus) of Cerebellum.
From Fig 141

the nucleus of the cerebellum.

In birds it appears as a very large tract extending from the vestibular nuclei to the internal nucleus of the cerebellum. In mammals it arises in the roof nucleus, curves forwards along the lateral wall of the fourth ventricle and ends in relation to the external vestibular nucleus. In the lower mammals it is a larger tract than in man, and bears a somewhat different relation in position to the superior cerebellar peduncle. (see p. 137).

Ferrier and Turner proved that this tract is an efferent tract from the roof-nucleus of the cerebellum to the vestibular nuclei and Bruce in an as yet unpublished paper read before the Medico-Chirurgical Society of Edinburgh, pointed out the great importance of this tract as a link between the sensory afferent tracts which end in the cortex of the middle lobe of the cerebellum and the vestibulo-spinal tract from Deiters' nucleus. The connection of these afferent and efferent systems is completed by the sagittal fibres of the cerebellum which pass between the cortex and the roof nucleus (see ~~diagram~~ Figs. 139-140). The connection thus established between the peripheral sensory nerves, the cerebellum, the vestibulo-spinal tract and the anterior-horn cells is evidently closely concerned in the maintenance of the equilibrium, a

Fo

Form.	Organ	Nuclei and Nerves. Cochlear:	Nuclei and Nerves. Vestibular	Central Connections
Fish. Elasmobranch	Duct still opens on surface of body Lagena small. Semicircular Canals large.	Undifferentiated -		(Lateral fillet ? - (Lat and Median Vestibulo Spinal. Tr
Fish. Teleost Large Cerebellum.	Auditory Organ shut off completely from Surface. Lagena Small. Semicircular Canals Large.	Two Lateral line Nuclei. Cochlear Root & Nucleus. One Lateral Line Nucleus	Vestibular Nucl. middle & Deiters Superior { Nebergangs ganglion	(Median. Longitud. Bundle (Lateral & Median Vestibulo Spinal Tra
Amphibian Small Cerebellum.	Inner Ear communicates with surface - by ossicle & Membrane. Lagena. Small. still. Semicircular Canals Small	Cochlear nucleus. Cochlear Nerve. No lateral line nuclei or Nerves	Vestibular Nucleus. Ext. { Superior = small middle = " Inferior - "	Lateral Fillet 1 Superior Olive. Ends in Torus Semicircular Lateral & Median Vestibulo. Spinal Tracts
Reptile Small Cerebellum.	Inner Ear communicates with Surface by ossicle & Membrane Large Cochlear (Sauropsid) Organ. Semicircular canals Relatively small.	Large Cochlear Nucleus Large Cochlear Nerve.	Vestibular Nucleus 1) External { Superior Small. Middle " Inferior " Root relatively small	Lateral Fillet 1 (Sup. Olive). ends in Post. Corp. Quad (Median and Lateral Vestibulo. spinal Tracts small.
Bird. Large Cerebellum +	Inner Ear. communicates with surface - as above. Cochlear organ = Small (Lagena) Cochlea spirally twisted Semicircular Canals well-marked.	Two cochlear Nuclei. 1 { Large - celled. 2 { Small - celled Cochlear Nerve Smaller Than Reptile's	Vestibular Nuclei 1) External { Superior Large, Middle " Inferior " 2) Internal { Dorsal. Large. Vestibular Nerve.	Lateral Fillet. 1 { Superior Olive 2 { Nucl. Corp Tra ends in Gl. Mesencephal No. Post. Corp. Quad 1 Dorsal 2) Median and 3) Lateral Vestibulo Spinal T
Mammal. Large Cerebellum.	Inner Ear connected with Surface by chain of ossicles & membrane Cochlear organ Large = Organ of Corti. Semicircular canals relatively Small.	Two. Cochlear Nuclei. (1) Tuberculum Acust. (2) Anterior Acustic Nucl. Both Large. Cochlear root relatively large.	Vestibular nuclei 1) External. { Superior = Small Middle = Large Inferior = Large 2) Internal (Dorsal. Vestibular root. same size as 3 smaller than cochlear.	Lateral Fillet 1 { Superior Olive 2 { Accessory Olive 3 { Nucl. Preolivary 4 { Nucl. Corp Trap Large. Post. Corp. Quad 1) Dorsal - 2) Median - 3) Lateral Vestibulo - Spinal Tra

view which is borne out by the intimate connection between the nerve from the semicircular canals, (the vestibular nerve) and Deiters' nucleus.

The other connections of the cerebellum have been described as far as is necessary for this thesis in the account given of the mammalian cerebellum and will not be further mentioned here.

A table is appended (p.180a) giving a synopsis of the development of the auditory organ and of its nerve. From this synopsis some interesting conclusions may be drawn:-

1. There is a progressive tendency to division and specialisation of organ and nerves into two parts, a vestibular and a cochlear, concerned respectively with equilibration and the sense of hearing.
2. That the development of the first system (the vestibular) is directly dependent upon the life-habits of the animal and varies according to this factor in different vertebrates, and even in different species of the same class of vertebrates. Thus it is well-marked in all actively-moving creatures, whatever their place in the scale of life, in bony fishes, in birds and in such mammals as the rat, the cat and man.

It is on the other hand very small in the creeping vertebrates,—the cyclostomes, some of the amphibia and the reptiles.

3. That in these creeping forms, the cerebellum is also very small.

4. That the cochlear system on the other hand shows a steady progression throughout the vertebrate series. In the skate it is a simple sense organ with an undifferentiated nucleus - in man it is a marvellously complex structure - the organ of Corti - with a special nerve and a complex series of nuclei. The only exception to this steady progress is in the case of the reptile, which has a more complicated cochlear organ than the bird, and a posterior corpus quadrigeminum which is not present in the bird. The cochlear organ of the reptile however, is a different organ from that of birds and mammals, and therefore, the reptile being excepted, the statement is true that there is a progressive development of the cochlear system from the lower to the higher vertebrates. In direct relationship with this increasing development of the cochlear organ, there is a growing complexity in its nervous centres and connections. The nucleus becomes larger and divides into two, and the secondary connections become

much more complex. Thus the corpus trapezoideum develops into a large tract instead of being represented by a few fibres, the superior olive becomes a convoluted nucleus with accessory nuclei, the lateral fillet gains steadily in size and its end-nucleus, the posterior corpus quadrigeminum, appears, and finally forms a large and conspicuous structure. (See diagram p/32.).

The eighth nerve system is thus seen to follow the general law that the elements of the central nervous system vary in proportion to the development of the parts they supply. It begins as an undifferentiated single nerve to a small sense organ, but as the sense organ develops its parts and modifies its function, the nerve and nuclei vary also, passing through many transitional stages to arrive at the complex nervous mechanism in connection with the cochlear and vestibular organs of the inner ear of mammals.

In conclusion I should like to take this opportunity of acknowledging my great indebtedness to Dr. Alexander Bruce, who suggested the subject of this thesis, and kindly gave me permission to carry out the practical part of the work in his pathological laboratory at Surgeons' Hall, Edinburgh.

Ayers. Journal of Morphology Vol. Vi. 1892. A contribution to the morphology of the vertebrate ear.

Beard. Branchial Sense organs in Ichthyopsida. Journal of Micros. Science. Vol. 26. 1886.

Ewart. Transactions. Royal Soc. Edinburgh 1891-92. Proceedings Royal Soc. London. Vol. XLV. 1889.

Allis. Journal of Morphology. Vol. II. 1890. The anatomy and development of the lateral line system in Amia Calva.

Mayser. Zeitschrift fur Zoologie. Vol. 36. Studien ueber das Gehirn de Knochen fische.

Goronowitsch. Morph. Jahrbuch Vol. XIII. 1888. Das Gehirn von Acipenser Ruthenus.

Platt. Journal of Micros. Science. Vol. 38 Ontogenetic differentiations of the Ectoderm in Necturus.

Assheton. Journal of Micros. Science. Vol. 38. Notes on the Ciliation of the Ectoderm of the Amphibian Embryo.

Ahlborn. Zeitschrift fur Zoologie. Untersuchungen ueber das Gehirn d. Petromyzonten.

Mayer. Anat. Anzeig. Vol. XIII. 1897. Das Centralnerven System v. Ammocoetes.

Strong. Journal of Morphology Vol. X.
The cranial nerves of Amphibia.

Köppen. Arch. f. Anal. (Ruchert) 1888 Zur Anatomie des Frosch Gehirns.

Kingsbury. Journal of Comparative Neurology 1897.
Structure etc., of the oblongata in fishes.

Johnstone. Anat. Anzeig. Vol. XIV. 1898. Hind-brain and cranial nerves of Acipenser.

Wallenberg. Anat. Anzeig Vol. XIV. 1898.
Die Secondäre Acusticuusbahn der Taube.

Brandis. Arch. f. Mikr. Anal. Vol. XLI. Unters. ueber das Gehirn der Vögel.

Kölliker. Gewebelehre d. Menschen. Vol II. First part.

Edinger. Vorlesungen ueber den Ban der Nervösen. Centralorgane.

Cajal. Beitrag z. Studium d. Medulla Oblongata.

Held. Arch. f. Mikr. Anat. vol.

Kolster. Studien uber das central Nerven-system. I.
Das Rückenmark einige Teleostier.

Thomas. Le Cervelet. Paris 1897.

Risien Russel. Phil. Trans. Royal Soc. London 1895.

Ferrier & Turner. Phil. Trans Royal Soc. London 1894.

Bruce. Illustrations of Mid and Hind Brain. On the Flocculus Brain 1895. Proc. Royal Soc. Edinburgh 1889.

Schaper. The finer structure of the Selachian cerebellum. Journal of Comparative Neurology. 1898. Vol. VIII.

Stroud. The Mammalian Cerebellum. Journal of Comparative Neurology 1895. Vol. V.